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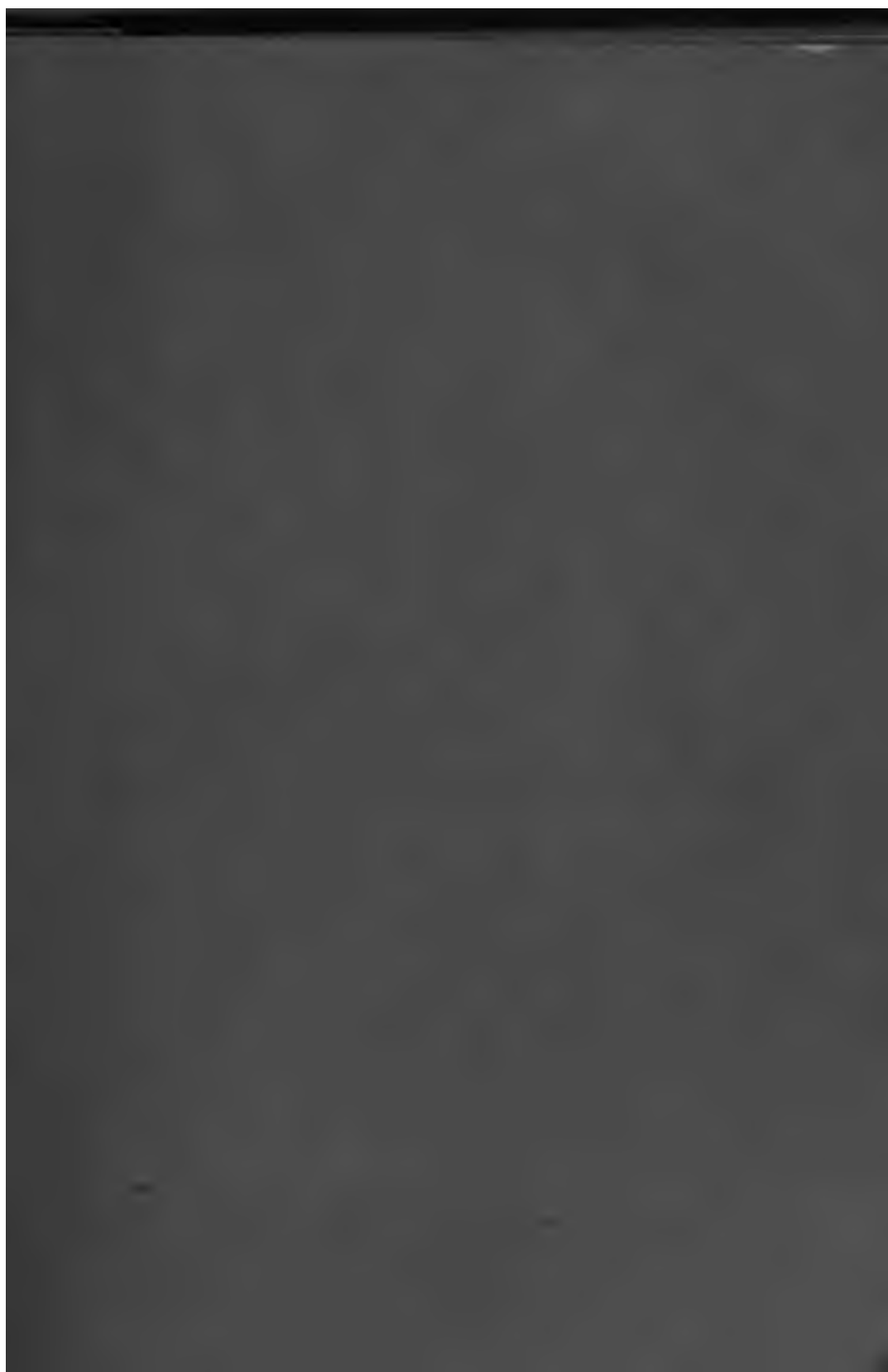


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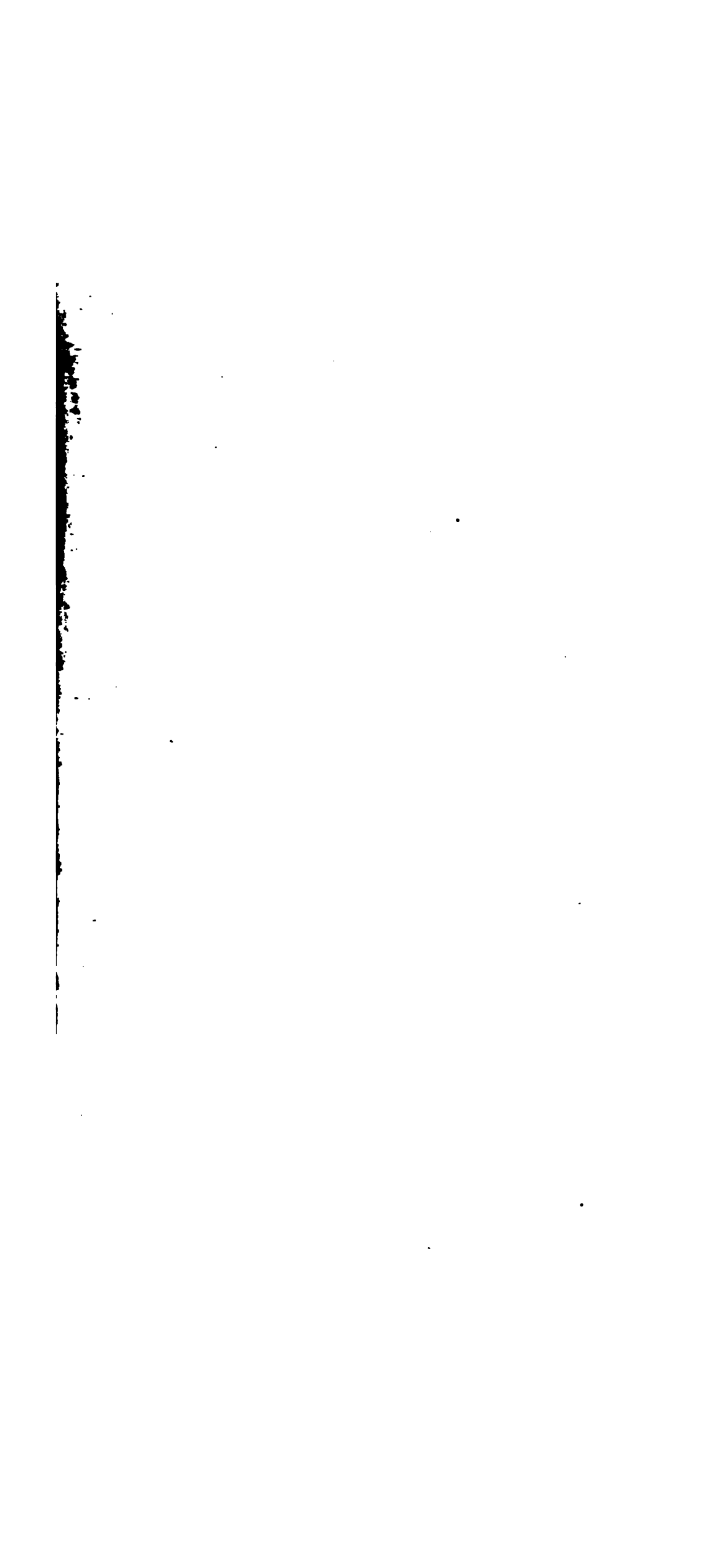
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87.

AN
INTRODUCTION
TO THE
STUDY OF EMBRYOLOGY.

BY
ALFRED C. HADDON, M.A. (CANTAB.), M.R.I.A.
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SCIENCE, DUBLIN.

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TO
The Memory
OF
HIS BELOVED MASTER AND FRIEND,
FRANCIS MAITLAND BALFOUR,
This Book
IS DEDICATED
BY
THE AUTHOR.

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PREFACE.

ALTHOUGH there are at the present time, in addition to the special accounts in various text-books of Human and Comparative Anatomy, two Students' Manuals in the English language solely devoted to the study of Embryology, it has appeared to me that a relatively small work, giving a general review of the subject, might prove of use to students.

A knowledge of the main facts of Comparative Anatomy and Systematic Zoology has been assumed for the reader, the book being especially designed for Medical Students, or for those who already possess a general acquaintance with the Animal Kingdom.

It will be noticed that many of the more difficult problems of Ontology and Phylogeny and special modes of development have either been merely alluded to or entirely ignored—as, for instance, the segmentation of the ovum and the formation of the germinal layers in Insecta and Teleostei. This has been of set purpose, as my main object in writing this book has been to give a brief connected account of the principal organs, omitting or barely mentioning structures and phenomena, which may be regarded as of secondary importance.

The facts of development have been largely supplemented by

hypotheses; and an endeavour has been made so to present the latter, that the student could not mistake them for the former.

It is inevitable that, in compiling such an introductory textbook as this, many subjects must be treated in a manner similar to that in which they have been dealt with by previous authors; and therefore I have not hesitated to borrow from them when occasion required.

In order to facilitate references, very recent, important, or doubtful observations have been associated in many cases with the investigator's name. It must be distinctly understood that I do not necessarily personally adopt statements or views which have been incorporated in the book; they are merely put forward for what they are worth.

The beginner is advised to pay attention only to the large type in the first reading, as purely theoretical subjects or matters of detail are printed in the smaller type. Most of the figures have been so drawn as to admit of their being coloured; and the student is recommended to tint each germinal layer and the organs derived from it in a uniform manner throughout the book: thus the epiblast and its derivatives might be coloured pink, and the hypoblast tinted blue. A uniform system of colouration will be found to be of great assistance to the memory.

The sources from which the figures have been taken are in all cases acknowledged, and in the cases where no source is given the illustrations are original. Figs. 40, 41, 44, 45, 80, 81, and 178* have appeared previously in the Proceedings of the Royal Dublin Society.

The classification adopted will be found in an Appendix. All the genera mentioned in the text have been inserted, in order that their systematic position may be seen at a glance.

A Bibliography has also been appended, which is designed to serve simply as a guide to the more recent literature, and no attempt has been made to render the list exhaustive. It will be noticed that most of the Memoirs cited are of later date than the year 1880. The more important earlier papers are recorded in the late Professor Balfour's "Treatise of Comparative Embryology." As any student who seriously studies Embryology must consult that invaluable work, I have considered it superfluous to repeat the Bibliography given by Balfour. The prevalent custom of authors of giving references to the literature of the subject under discussion renders it comparatively easy to discover what has already been written thereon.

Finally, I would here express my warmest thanks to my friend Professor G. B. Howes, of the Normal School of Science, South Kensington, for his kindness in reading the proofs and in making many valuable suggestions.

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AN INTRODUCTION TO THE STUDY OF EMBRYOLOGY.

CHAPTER I.

MATURATION AND FERTILISATION OF THE OVUM.

Introduction.—Embryology is the term usually applied to the whole cycle of changes undergone by an animal in passing from an egg to the adult condition. It is, in other words, the History of its Development.

The name of embryo (or foetus, in mammalian embryology) is restricted to the unborn young. At birth the young may closely resemble the parent, or be very dissimilar; in the latter case, it is known as a larva, and undergoes a series of changes or a metamorphosis before it attains the adult state.

Even closely allied animals may be "born" at very different stages in their development; the higher animals are, however, generally born at a relatively later stage than those lower in the animal scale. They are thus better fitted for the struggle for existence, and expend less energy during their development than if they had to provide for themselves.

In the higher animals the young also have the further advantage of the watchful care of their parents, a factor which must have materially influenced the evolution of the race.

Embryology may be studied under two aspects. The first, or **Ontogeny**, deals solely with the history of the individual, and traces the development of the animal as a whole, and of its various organs.

The second, or comparative aspect, compares the development of animals, and taking those phases which are common to all or

to many, attempts therefrom to deduce or reconstruct the evolution of the animal kingdom. This study is known as **Phylogeny**.

The chief result of all embryological inquiry has been to demonstrate that the history of the individual recapitulates in its main features the evolution of the race, and thereby to give positive evidence in favour of the Theory of Evolution, in the general acceptance of the term.

It is very important to bear in mind that larval forms, as well as adults, have to adapt themselves to external conditions, and that they are consequently liable to be variously modified, and, within limits, to be highly specialised. These modifications often have no relation to the adult structure, and consequently can have no phylogenetic significance.

Some preliminary knowledge of Zoology and Comparative Anatomy is necessary in order to appreciate fully the phases in the development of any one animal, and it is, of course, essential in studying the general principles of Embryology, as constant reference must be made to the structure of different forms. Such a knowledge will be assumed for the readers of this book.

The Animal Kingdom is divided by zoologists into the **Protozoa**, or unicellular animals, and the **Metazoa**, or those animals composed of a number of cells so united together as to form tissues. As the latter alone produce ova or eggs, the science of Embryology deals solely with the Metazoa. Although there is considerable variation in the details of the classification of the Metazoa, zoologists are tolerably well agreed upon the main divisions, and in this work that classification and terminology are adopted which are in most general use in English-speaking countries.

Reproduction amongst the Protozoa consists in a direct or indirect method of cell-division, each product of such division forming a new individual (fig. 1, B, C, D). This process may, or may not, be preceded by a temporary apposition or permanent fusion of two or more individuals. The conjugating individuals may either be apparently quite similar (fig. 1, E), or may exhibit certain differences (fig. 1, F); but conjugation is always effected between forms which are similarly motile—that is, ciliated individuals invariably conjugate with ciliated, and amœboid with other amœboid, forms. Even among those Flagellate Infusoria which pass through a comparatively complicated life-history, an individual in the flagellate stage never conjugates with another in

the amœboid condition. Active reproduction of one kind or other usually occurs after conjugation.

Some Protozoa form compound masses, but the individuals composing the colony are, with rare exceptions (Proterospongia), similar to one another, and have a practically independent existence.

Although asexual reproduction by various modes of budding and fission is known in nearly all the groups of the Metazoa, the sexual method is of invariable occurrence. The essential act of

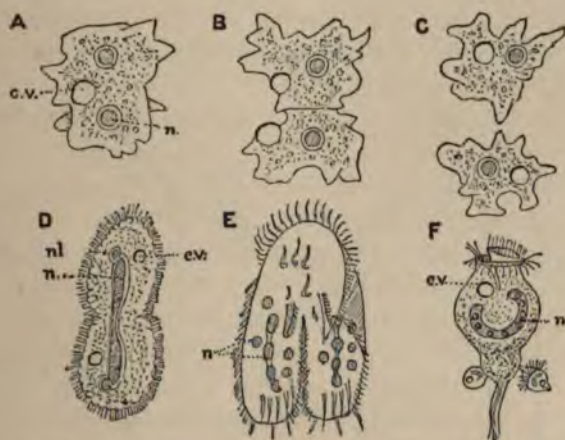


FIG. 1.—REPRODUCTION AMONGST PROTOZOA. Not drawn to scale.

- A-C. Fission in an Amoeba. A. The nucleus has divided into two. B. Two contractile vacuoles have also formed and the protoplasm is dividing. C. The process is complete. [After Hovees.]
 D. Fission in *Paramecium bursaria*. There are two contractile vacuoles and two paramecia, but the nucleus has not yet completely divided.
 E. Conjugation of *Stylonychia mytilus*, illustrating also the fragmentation of the nucleus.
 F. Conjugation of *Vorticella microstoma*. Two free-swimming microzooids have attached themselves to a fixed form. They all possess a curved nucleus and a contractile vacuole. [D-F after Stein.]

c.v. contractile vacuole; n. nucleus; nl. paranucleus.

this form of reproduction consists in the fusion of a flagellate cell or spermatozoon with an amœboid cell, the egg or ovum (figs. 10 and 11).

In a very few cases the spermatozoa are either amœboid, as in Nematodes, some Arachnids, and *Limulus*, or often passive and rayed, as in most Crustacea; but in the great majority of animals the spermatozoa are flagellate and actively motile (fig. 2).

The ovum, under very rare and exceptional conditions, may develop into a new organism *without* previous fertilisation by a spermatozoon; this phenomenon is known as *parthenogenesis*.

The ovum and spermatozoon unite to form the fertilised ovum or *oosperm*, which then undergoes rapid cell-division; the cells thus produced remain in contact with one another, and though at first usually very similar, certain groups of cells soon take upon themselves definite characters, and thus initiate the primitive tissues.

Accepting the view that the Metazoa were derived from colonial Protozoa, it follows that every cell of the primitive Metazoa was capable of forming fresh colonies by



FIG. 2.—SPERMATOOA [from various sources]. Not drawn to scale.

1. Sponge; 2. Hydroid; 3. Nematode; 4. Crayfish; 5. Snail; 6. Electric Ray; 7. Salamander; 8. Horse; 9. Man. In many spermatozoa, as in Nos. 7 and 9, an extremely delicate vibratile band is present.

cell-division. Many Metazoa possess the power of asexually producing new forms by fission or by budding; but the tissues implicated in this process must be regarded as being essentially undifferentiated in character.

Owing to the advantage derived from physiological differentiation of labour, the reproductive function came to be chiefly retained by certain cells, the remainder specialising along other lines. Those cells which pre-eminently retain the reproductive function are restricted in their position, and the tissue which they constitute (the germinal tissue) is contained within what is known as a *generative organ* or *gland*. When ripe, the germ-cells become detached, and commence a free existence.

After fertilisation, the ovum, or the embryo into which it develops, is in a few cases retained within the oviduct of the mother for a longer or a shorter period, and may temporarily even be intimately, but very rarely structurally, connected with the walls of the oviduct or uterus, as will subsequently be described.

The primitive germ-cells of animals are, practically, precisely similar to one another (fig. 175), and, when first recognisable as germ-cells, it is impossible to tell whether they will develop into ova or sperm-cells. In this connection it is suggestive to find that both the ovaries and the testes in *Sagitta* are developed from a single primitive germ-cell, which makes its appearance at a very early stage of development. The primitive germ-cells may more especially be said to correspond to the Protozoon ancestors of the Metazoa.

Before dealing further with the history of the germ-cells, however, it will be advisable to describe briefly their mode of origin.

The Ovum.—The primitive ova usually form part of a definite epithelium, of which most of the cells, or it may be only a very small number, develop into ripe ova. The germinal epithelium is well supplied with nutritive fluid (either blood or the fluid contents of the cavity of the body), which serves for the growth of the ova. From the nutriment thus provided the ova generally store up a greater or less amount of reserve food-material, which is known as "*yolk*" or "*food-yolk*."

It would be foreign to the purpose of this work to enter into a comparative account of the development of ova from primitive germinal-cells. As a general rule, certain of the cells of the germinal epithelium are directly converted into ova. In Vertebrates, the germinal epithelium is borne upon a distinct germinal ridge; the epithelium increases in thickness, and becomes broken up into cords or trabeculae (ovarian tubes of Pflüger), which, by mutual ingrowth, lie in the stroma or mesoblastic core of the germinal ridge. Isolated masses or nests may also be formed (fig. 3).

Balfour has shown that in Elasmobranchs and other forms, in addition to the foregoing or direct origin of the ova, the protoplasm of the cells forming the nests fuses into a single mass containing the nuclei of the previously distinct ova. Various changes are undergone, but eventually a few of the nuclei segregate protoplasm round themselves to form the ova, the remainder having broken down to pabulum for the permanent ova.

Beddard finds that in *Protopterus* two kinds of ova are developed—(a.) The ovum is a mass of granular protoplasm, containing a germinal vesicle limited by a distinct membrane, inside of which is a peripheral layer of germinal spots. Later the protoplasm becomes vacuolated, and largely differentiates to form yolk-granules. (b.) The ovum arises from the fusion of a nest of germinal cells lying within a follicle; not only is yolk formed within the central mass, but it is also produced within the columnar cells of the follicular epithelium. These cells proliferate and migrate into

the interior of the ovum; eventually they disappear. The yolk of these ova appears to be largely derived from the follicular cells.

The yolk consists of highly refractive particles, which vary considerably in their appearance and structure. As a rule, the yolk elements are small vesicles, which usually contain smaller vesicles and other bodies (fig. 28, *v*). In Birds the whole of the yolk at first consists of these white yolk spheres; but during the development of the egg, some of the white yolk spheres become modified to form the yellow yolk (fig. 28, *a* and *c*). In the ripe unincubated egg the yellow yolk constitutes the great mass of the "yolk," the white yolk being restricted to a peripheral and several concentric layers, and to a central mass which extends in a constricted neck, and again widens out to form a bed, upon which the blastoderm rests (fig. 28, *A*, *w*, *y*).

It not unfrequently happens (many Hydrozoa, Insects, some Vertebrates, &c.) that certain of the primitive germ-cells feed upon neighbouring germ-cells, so that the growth of the ovum



FIG. 3.—SECTION THROUGH A PORTION OF THE OVARY OF A MAMMAL. Illustrating the mode of development of the Graafian follicles. [From Wiedersheim.]

D. discus proligerus; Et. ripe ovum; G. follicular cells of germinal epithelium; g. blood-vessels; K. germinal vesicle (nucleus) and germinal spot (nucleolus); KE. germinal epithelium; Lf. liquor folliculi; Mg. membrana or tunica-granulosa or follicular epithelium; Mp. zona pellucida; PS. ingrowths from the germinal epithelium, ovarian tubes, by means of which some of the nests retain their connection with the epithelium; S. cavity which appears within the Graafian follicle; So. stroma of ovary; U. theca folliculi or capsule; U. primitive ova. When an ovum with its surrounding cells has become separated from a nest, it is known as a Graafian follicle.

and its store of food-yolk are made at the expense of its fellow germinal cells. In most Platyhelminths that portion of the primitive germinal epithelium which is destined to provide pabulum for the ova proper is separated from the ovary as *yolk-glands*, or *vitellaria*, and their products, *yolk-cells* or *yolk-granules*, surround the ova after they have left the ovary, and before they are enclosed within the egg-capsules. The yolk-cells may be regarded as germinal cells which have lost the power of reproduction, but retained that of forming yolk. Either the ovum or the embryo in due course feeds upon this reserve of food.

When many ova are deposited within the same egg-capsule as in some forms of Prosobranch Gastropods (*Buccinum*), the more

advanced embryos devour those that are imperfectly developed, so that a very limited number, sometimes only a single individual, eventually escape from one capsule.

The fusion of several germinal cells with one ovum does not correspond to the multiple conjugation of some Protozoa, as in the



FIG. 4.--DIAGRAMS OF OVA [from various sources after Geddes]. Not drawn to scale.

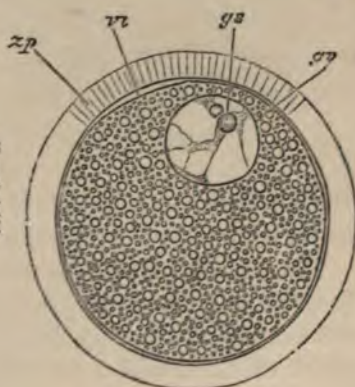
a. Diagram of a typical ovum with a delicate egg-membrane, granular protoplasm, nucleus (germinal vesicle), and nucleolus (germinal spot). b. Amoeboid ovum of Hydra [after Kleinenberg]. c. Early ovum of a Sea-Urchin (*Toxopneustes variegatus*) with pseudopodia-like processes extending into the gelatinous egg-membrane (vitelline membrane) in order to obtain nutriment from without; afterwards they become much finer and more regular, causing the vitelline membrane to have a striated appearance; hence it is termed the "Zona radiata"—the striae are really delicate pores [after Selenka]. d. Nearly ripe ovum of *Strongylocentrotus lividus* with its zona radiata [after Hertwig].

formation of plasmodia; it is merely the assimilation of several cells by one ovum, much as an *Amoeba* feeds upon its prey.

An ovum is a small free cell which is characterised in the resting-stage by possessing a large clear nucleus, the germinal vesicle, and a well-marked highly refractive nucleolus, the ger-

FIG. 5.—OVUM OF THE CAT. Highly magnified; semi-diagrammatic. [From Quain, after Schäfer.]

gs. germinal spot; gv. germinal vesicle; vi. vitellus, or protoplasm of ovum filled with yolk granules, round which a delicate membrane was seen; zp. zona pellucida (*Zona radiata*); only a few radial pores are drawn.



minal spot; in many cases several germinal spots occur. Figs. 4 and 5 illustrate various kinds of ova.

The protoplasm usually has, as has just been mentioned, the power of storing up albuminoid matter as reserve food material by a differentiation of its own substance in the form of yolk-granules or spheres. The amount of food-yolk varies greatly; in some few

instances none appears to be differentiated; often only a little is formed; more frequently there is a considerable amount; and in the eggs of Elasmobranchs and of Sauropsida an enormous quantity is deposited. The distribution of the yolk within the egg also varies, being either chiefly concentrated at one pole (*telolecithal*), or towards the centre (*centrolecithal*), or evenly distributed throughout (*alecithal*).

As the amount of protoplasm in an ovum containing much food-yolk is relatively small, the storing of the yolk-granules within its substance would naturally cause it to be distended. In those ova with a very large amount of yolk, the protoplasmic reticulum scarcely more than serves to keep the yolk-granules together

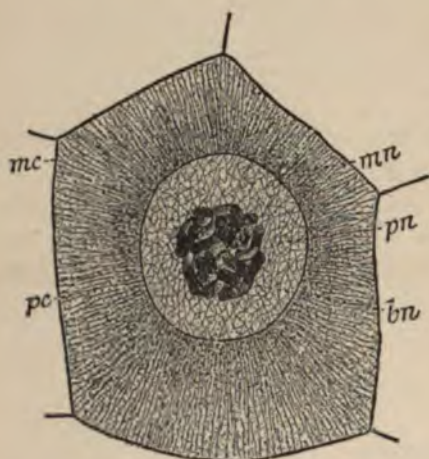


FIG. 5*.—TYPICAL CELL AND NUCLEUS OF THE INTESTINAL EPITHELIUM OF A FLESH-MAGGOT (*asticot*), treated with osmic acid vapour. [From Carnoy.]

bn, continuous band of nucleine, contracted to the centre of the nucleus, and showing numerous twists; *mc*, membrane of the cell; *mn*, membrane of the nucleus; *pc*, protoplasm of the cell, showing the radiating reticulum and the *enchylema* enclosed in its meshes; *pn*, plasma of the nucleus, showing a reticulum and a plasmic *enchylema*, as distinct as those of the protoplasm.

The structure of an ovum is practically identical with that of such a tissue-cell as the above.

During development, certain cells of the embryo reconvert the food-yolk into active protoplasm.

The *germinal vesicle* of the unripe ovum, as Carnoy points out, has the same general structure as the ovum itself; that is, it consists of an extremely fine protoplasmic *reticulum*, the meshes of which are filled with a granular fluid (*enchylema*). The reticulum also forms a delicate nuclear membrane. But, in addition to the above, the nucleus possesses a distinctive substance, which is variously termed *nucleine*, *nucleoplasm*, or, from its being readily stained by the action of certain reagents, *chromatin*. In very young ovarian ova, the chromatin occurs in the form of a very long, extremely and irregularly contorted thread or nuclear filament.

The nuclear filament is condensed in more mature ova into a

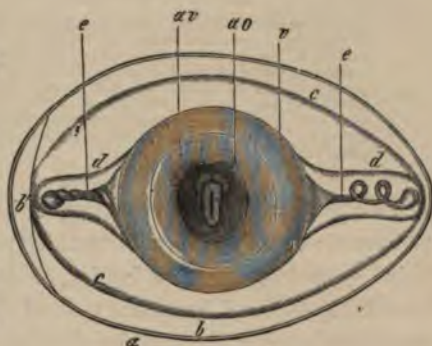
single spherical mass, the *germinal spot*, or into a few or a large number of smaller germinal spots.

Ova may be either naked (fig. 4, A and B), or surrounded by one or more membranes (fig. 4, C, D, and fig. 5). The primary egg-membranes (*vitelline membranes*) are usually differentiated from the protoplasm of the ovum itself.

In Vertebrates two egg-membranes are usually present, an external delicate *vitelline membrane*, which is probably formed by the ovum itself, but in some cases a similar membrane may be secreted by the epithelium of the ovarian follicle. This membrane is often termed a *chorion*. Below the vitelline membrane a thicker membrane, perforated by innumerable fine radial pores, is differentiated out of the peripheral layer of the ovum. It is known as the *zona radiata* or *zona pellucida*. The secondary egg-membranes are either

FIG. 6.—A FOWL'S EGG AFTER ABOUT THIRTY HOURS' INCUBATION. Viewed from above, the upper portion of the shell being removed. [From Kölliker after Von Baer.]

" a. shell; b. shell-membrane; b'. air-chamber at broad end of egg between the two layers of the shell-membrane; c. the boundary between the outer and middle portion of the albumen; d. the internal layer of more fluid albumen, which also extends round the yolk as a thin sheath; e. chalaza; e'. vitellus or yolk; av. area opaca, or that portion of the blastoderm which extends over the yolk; the heart-shaped central portion, ao, is the vascular area of the area opaca. In the centre is the embryo surrounded by the area pellucida.



secreted by accessory generative glands, or by the glandular wall of the oviduct. When a secondary egg-membrane is impregnated with calcareous deposits, it is known as an egg-shell. The secondary egg-covering often encloses an albuminous glairy fluid—the white of egg—which serves for the protection and further nutriment of the embryo (figs. 6, 74, 75). The albumen also is secreted, either by special glands (most Invertebrates), or by the wall of the oviduct (Vertebrates).

Maturation of the Ovum.—Before or after fertilisation, certain changes, which are of considerable interest, take place in the ovum. The germinal vesicle often becomes amœboid, and passes to one pole of the ovum, and the germinal spot disappears (fig. 7, B-D); in fact, both the germinal vesicle and spot disappear as such, and pass into those karyolytic figures which characterise cell-division (see p. 18).

The resulting nuclear spindle is placed vertically, the peripheral nuclear star, or "aster," being situated in a small protuberance from the surface of the ovum. This process is segmented off from the ovum, and a minute cell is formed, containing a portion of both the protoplasm and the nucleus of the parent-cell (fig. 7, F and L).



FIG. 7.—FORMATION OF POLAR CELLS IN A STAR-FISH (*Asterias glacialis*).
[From Geddes, A-K after Fol, L after O. Hertwig.]

A. Ripe ovum with excentric germinal vesicle and spot; B-D. Gradual metamorphosis of germinal vesicle and spot, as seen in the living egg, into two asters; F. Formation of first polar cells and withdrawal of remaining part of nuclear spindle within the ovum; G. Surface view of living ovum in the first polar cell; H. Completion of second polar cell; I. A later stage, showing the remaining internal half of the spindle in the form of two clear vesicles; K. Ovum with two polar cells and radial striae round female pronucleus, as seen in the living egg. [E, F, H, and I, from picric acid preparations.] L. Expulsion of first polar cell.

This phenomenon is repeated, and two cells are budded off from the ovum; these are known as the "*polar cells*" (or as polar bodies, polar globules, directive bodies, &c.), from the fact that they are invariably derived from that pole of the ovum at which the epiblast or upper-layer cells will be developed; hence, also, this pole is



FIG. 8.—FORMATION OF POLAR CELLS IN OVUM OF *ELYSIA VIRIDIS*.

The upper pole of the ovum becomes amoeboid during the formation of the polar cells. The second polar cell is in process of formation.

usually termed the *upper pole* of the ovum (see figs. 12 and 17). During the production of the polar cells, the ovum, especially at its upper pole, may exhibit amoeboid movements; this is well shown in the ovum of *Elysia* (fig. 8).

Although the polar cells may remain attached to the developing

ovum for some time, they take no share in the formation of the embryo, and are simply to be regarded as superfluous bodies.

What remains of the primitive nucleus passes towards the centre of the ovum, usually in an inactive or resting condition, being without radial striæ. It is known as the *female pro-nucleus*.

The ovum is now in a passive condition, and ready to be fertilised. The extrusion of the polar cells, though occasionally taking place *after* fertilisation (ex. *Elysia*, fig. 8), is really to be regarded as the last term in that series of changes which occurs *before* impregnation, and to be, in fact, anticipatory of it.

Before following the history of the ovum further, it will be necessary to return to the sperm-cells.

The Spermatozoon.—Although we find considerable variation in certain details of structure, there is a general similarity in the appearance of the spermatozoa of animals, a head and vibratile tail being of almost universal occurrence: the most important exceptions have already been mentioned (p. 3 and fig. 2).

The primitive sperm-cells or mother-cells of the spermatozoa arise from a tissue corresponding to that which gives origin to the primitive ova (p. 242, fig. 175). The exact manner in which the spermatozoa are developed varies in different animals, and has been variously described by numerous investigators. This being the case, it will be advisable to give simply a sketch of what appear to be the most important facts in *spermatogenesis*, as this process is termed.

Those cells of the generative epithelium which develop into male sexual cells undergo cell-division in the ordinary manner, and may give rise to a considerable number of cells (*spermatoblasts*). Each spermatoblast is converted into a spermatozoon, and, in doing so, gives rise to a small mass of protoplasm, the so-called *seminal granule*, or globule, or accessory corpuscle, which appears to have no further function. Fig. 9, A-H, illustrates this process in the Rat.

Instead of becoming distinct, the spermatoblasts or incipient spermatozoa may remain aggregated together (*spermosphere* or *sperm-morula*), and surround a central non-nucleated protoplasmic mass (the *sperm-blastophore*), as in the case of the Snail and Earthworm (fig. 9, O-S).

In Elasmobranchs (fig. 9, I-X) the nucleus of the sperm-cell (sometimes called the *spermatocyst*) alone divides, forming a number of daughter-nuclei, the remains of the parent-nucleus still persisting. The protoplasm of the cell differentiates into the tails of the spermatozoa, while the daughter-nuclei constitute the main portion of their heads. The ripe spermatozoa are liberated by the rupture of the wall of the sperm-cell, leaving behind the parent-nucleus and a small remnant of unused protoplasm. This latter is merely an abbreviated variation of the former process, and the residual nucleus and protoplasm clearly correspond to the accessory corpuscle or to the sperm-blastophore in the preceding forms.

The nucleus of each daughter sperm-cell constitutes the head of a spermatozoon; it is surrounded by an extremely delicate film, which is produced from one end into a fine flagellum, and sometimes also into an almost imperceptible undulating membrane; these are formed by the protoplasm of the spermatoblast. Every spermatozoon is thus a true morphological cell.

Kölliker, however, maintains that the entire mammalian spermatozoon is simply a free nucleus.

Fertilisation of the Ovum.—It is needless to recount the various ways by which spermatozoa may reach ova; suffice it to say, that either within the female or in the surrounding water a

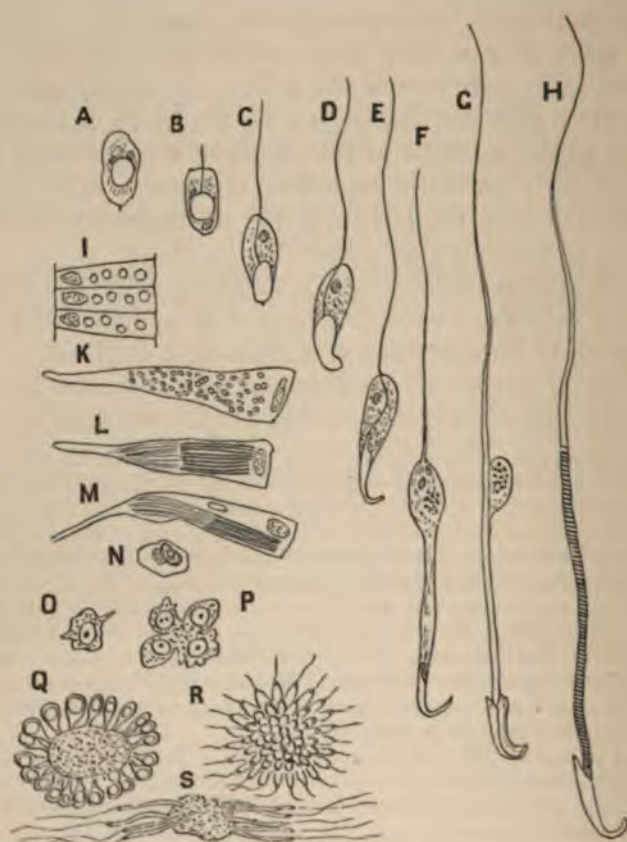


FIG. 9.—SPERMATOGENESIS

A-H. Isolated sperm-cells of the Rat, showing the development of the spermatozoon, and the gradual transformation of the nucleus into the spermatozoon head. In G the seminal granule is being cast off. [After H. H. Brown.]

I-M. Sperm-cells of an Elasmobranch. The nucleus of each cell divides into a large number of daughter-nuclei, each one of which is converted into the rod-like head of a spermatozoon.

N. Transverse section of a ripe cell, showing the bundle of spermatozoa and the passive nucleus. [I-N after Semper.]

O-S. Spermatogenesis in the Earthworm: O. young sperm-cell; P. the same divided into four; Q. spermatosphere with the central sperm-blastophore; R. a later stage; S. nearly mature spermatozoa. [After Blomfield.]

spermatozoon comes into contact with an ovum, and either penetrates any membrane which may surround it, or passes through an aperture (*micropyle*) left in the egg-membrane.

When the spermatozoon is approaching the actual surface of an

ovum, a process from the latter sometimes rises up to meet it, and a fusion is effected (fig. 10, A-D, and fig. 11, A). The head of the spermatozoon penetrates the ovum, while the tail, after vibrating feebly, is absorbed.

The head, or rather the nucleus of the spermatozoon, is converted into an aster or star, and is now known as the *male pro-*



FIG. 10.—FERTILISATION OF OVUM OF A STAR-FISH (*Asterias glacialis*). [From Geddes after Fol.]

In A-D the spermatozoa are represented as imbedded within the mucilaginous coat of the ovum. In A a small prominence is rising from the surface of the ovum towards the nearest spermatozoon; in B they have nearly met, and in C they have met. D. The spermatozoon has penetrated the ovum, and a vitelline membrane with a crater-like opening has been formed, which prevents the entrance of other spermatozoa. H. ovum showing polar cells and approach of the male and female pro-nuclei; the protoplasm is radially striated round the former. E, F, G. later stages in the coalescence of the two nuclei.

nucleus. It travels towards the female pro-nucleus, which, it will be remembered, is situated in the centre of the ripe ovum (fig. 10, H). The female pro-nucleus becomes somewhat amœboid, and fusion occurs between the two elements, thus forming a new nucleus (fig. 10, E-G). While this is taking place, the ovum itself often exhibits amœboid movements (fig. 11, A).

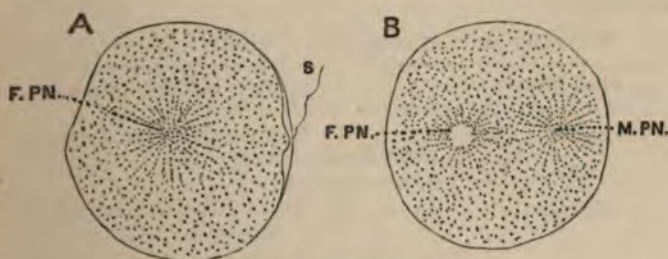


FIG. 11.—FERTILISATION OF OVUM OF *ELYTHIA VIRIDIS*.

A. ovum sending up a protuberance to meet the spermatozoon; B. approach of male pro-nucleus to meet the female pro-nucleus; F.P.N. female pro-nucleus; M.P.N. male pro-nucleus; S. spermatozoon.

The fertilised ovum is a very different body from the primitive ovum, as it consists of a portion of the original protoplasm and nucleus of the latter reinforced by those of another cell, which is usually derived from a different animal. The new nucleus is called the *segmentation nucleus*, and it may be well to adopt Bal-four's name of *oosperm* for the fertilised ovum.

There is some doubt whether the male pro-nucleus has the full value of a true nucleus, and this has led Flemming to define fertilisation as the union of "the chromatin of a male with that of a female nuclear body." Van Beneden has recently shown that the essential act of fertilisation consists in the grouping together (or probably, more accurately, of the fusion) of the chromatin or germ-plasma of the nucleus of the spermatozoon with that of the nucleus of the ovum. During the first division of the oosperm, and in all the succeeding phases of segmentation, each new cell receives an equal share of the paternal and maternal chromatin. (See chap. ii. p. 19, and fig. 13.)

The fertilisation of an ovum by a spermatozoon is paralleled by the permanent conjugation of such Protozoa as *Vorticella* and many Monads. In each case the phenomenon is followed by rapid cell-division—the resulting cell-units remaining separate in the Protozoa, whereas they group themselves together so as to form an aggregate of a higher series in the Metazoa.

Significance of the Maturation and Fertilisation of the Ovum.—There have been numerous speculations concerning the significance of the polar-cells. The view now generally accepted is that first propounded by Minot, and subsequently (but independently) proposed by Balfour, which suggests that the polar-cells represent what may be regarded as the male element of the primitive germinal cell, the sexes not being supposed to be differentiated in the latter. The ovum is thus preparing itself for the reception of a vigorous element derived from a different source. Similarly, the accessory corpuscle, or its equivalent, is regarded as the female portion of the primitive sperm-cell, the remaining nuclear matter and protoplasm being used up in the manufacture of unisexual (male) cells. The mature ovum, being unisexual, is free to conjugate with a male cell. The two are mutually complementary, and after union constitute a single perfect unit.

The relations between the male and female elements may, according to this view, be thus tabulated:—

Indifferent germinal cells, which eventually specialise into	
ovum (oospore),	sperm-cell (spermospore).
Each by cell-division develops into	
(oosphere),	(sperm-morula) spermosphere,*
which is composed of	
A. a passive element,	
polar-cells,	sperm-blastophore (seminal globules or granules);
B. an active sexual element,	
mature ovum,	spermatoblasts, which are directly converted into spermatozoa.
The union of the latter constitutes the fertilised ovum (oosperm).	

Minot proposed the common term of *thelyblast* for a mature ovum and for a sperm-blastophore, and *arsenoblasts* for the polar-cells and spermatozoa. Sexual reproduction would thus consist in the union of a *thelyblast* from one source with an *arsenoblast* from another source.

* In Mammals the sperm-cell gives rise to spermoblasts, each of which gives off a seminal globule, the remainder differentiating into a spermatozoon.

Unfortunately, the terms employed in describing the various stages in the development of the generative elements are not used in a synonymous sense by the various investigators and writers on the subject; those in the most general use have been here adopted.

A more simple view is that the extrusion of the polar-cells prevents the parthenogenetic development of the egg, merely by eliminating a considerable quantity of nuclear matter. The researches of Van Beneden on *Ascaris* have demonstrated in a quantitative manner the amount of chromatin thus lost; the precise amount for *Ascaris* being three-fourths of that present in the nucleus of the ovarian ovum.

The spermatozoon supplies a sufficient amount of new chromatin to enable the embryo to develop. According to this view, there is no essential distinction between the chromatin of the male as opposed to that of the female germ-cell.

At the end of this work will be found a summary of Weismann's and Geddes' conclusions respecting the significance of the maturation and fertilisation of the ovum.

The next series of changes undergone by the oosperm is that known as *segmentation*. The unicellular oosperm divides, by ordinary cell-division, into a large number of cell-units. The resulting mass is a multicellular organism, whose "life" consists of the sum-total of the activities of its component cells. It is thus an individual of a higher order than a Protozoon, and one possessing an infinitely greater capacity for progressive evolution.

CHAPTER II.

SEGMENTATION AND GASTRULATION.

ON the cessation of the various phenomena related above, the oosperm becomes spherical in contour, and its nucleus reappears as a clear rounded vesicle, enclosing a distinct round nucleolus.

This nucleus is properly termed the "*segmentation nucleus*," as it differs fundamentally from the original nucleus of the unfertilised ovarian ovum. The name "germinal vesicle," which is commonly applied to the nucleus of ova, is open to the objection that it is used indiscriminately for the nucleus both before and after fertilisation; it will here be confined to the former condition.

A.—Invertebrates.—Typical or Alecithal Segmentation.—

In order to gain a clear comprehension of the segmentation of the oosperm, it will be advisable to take as an example a form in which the process is not obscured by secondary details. The early stages of segmentation can be readily studied in the eggs of most Fresh-water Molluscs. The Nudibranch Mollusc *Elysia viridis* also serves very well for this purpose; and the following account refers to the segmentation, as seen in the living egg, of that form.

After a resting-stage, the nucleus divides into two, the nucleolus having immediately before similarly divided (fig. 12, A-C), and each new nucleus travels to an opposite pole of the oosperm. Whilst this is taking place, the nuclei, as such, disappear; being apparently replaced by two stars, some of the rays of which meet one another in the middle line. These *polar stars*, as they are termed, are composed of the radially arranged granular protoplasm of the cell. The polar stars then entirely separate, and the oosperm usually becomes distinctly amœboid, especially at its upper pole. A shallow groove makes its appearance on the surface of the oosperm midway between the two nuclear foci. The groove rapidly deepens (fig. 12, D, E), and eventually divides the oosperm into two distinct spherical halves, which immediately afterwards become appressed together. The nucleus has by this time reappeared as a clear spot

in the centre of each polar star; the rays of the latter disappear and the chromatin collects to form a new nucleolus (fig. 12, F, G). Each segmentation sphere now passes through a short resting-stage.

The application of staining reagents reveals the nature of the changes undergone by the nucleus in segmenting oosperms. In all cases the nucleus is transformed into a spindle-like arrangement of delicate fibres, termed the "*nuclear spindle*," round the apices of which the cell-protoplasm radiates as the above-mentioned polar stars. The chromatin aggregates at the centre of each fibre, and divides transversely into two, each moiety travelling along its own

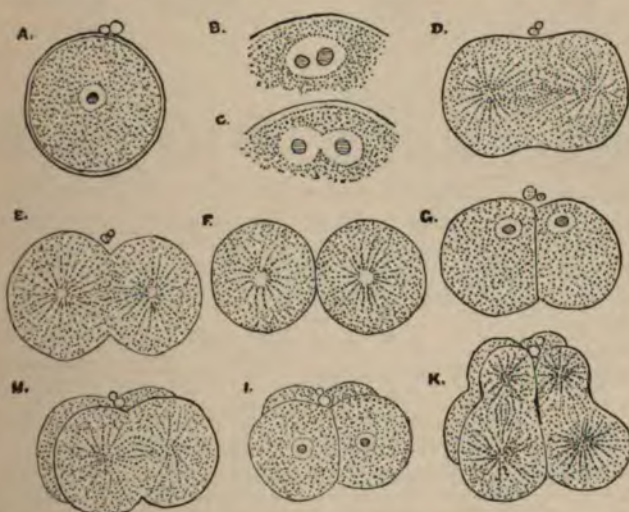


FIG. 12.—EARLY STAGES OF SEGMENTATION OF ELYSIA VIRIDIS (drawn from the living egg).

A. oosperm in state of rest after the extrusion of the polar cells; B. the nucleolus alone has divided; C. the nucleus is dividing; D. the nucleus, as such, has disappeared, first segmentation furrow appears; E. later stage; F. oosperm divided into two distinct segmentation spheres, the clear nuclear space in the centre of the aster of granules is growing larger; G. resting-stage of appressed two spheres; H. I. similar stages in the production of four spheres; K. formation of eight-celled stage.

fibre towards the nearest apex of the nuclear spindle (fig. 13, *d-f*). The fibres between the two receding masses of chromatin thin out, and eventually disappear. Finally, the nuclear substance segregates into an ordinary resting nucleus and nucleolus.

The Behaviour of the Nucleus in Cell-Division.—The behaviour of the nucleus during cell-division has received a great deal of attention within the last few years; and as it is a subject of considerable importance, it will be advisable to give a brief account of the process.

The nucleus of a typical tissue-cell consists of a rounded vesicle containing a nuclear matrix, which is termed "*achromatin*," as it is only lightly coloured on the

application of staining reagents. The achromatin is permeated by a delicate network or reticulum of a denser substance, the "nucleoplasm" or "chromatin," which also forms the delicate wall of the vesicle. This network readily stains deeply, and the intersections of the fibres usually give a dotted appearance to the nucleus. When the cell is in a resting condition, the chromatin is, as a rule, concentrated either into several rounded bodies, or more frequently into a single mass, the nucleolus; but this is usually, if not always, connected with the wall of the nucleus by delicate strands of chromatin.

During the process of division in such a nucleus as that just described, the con-

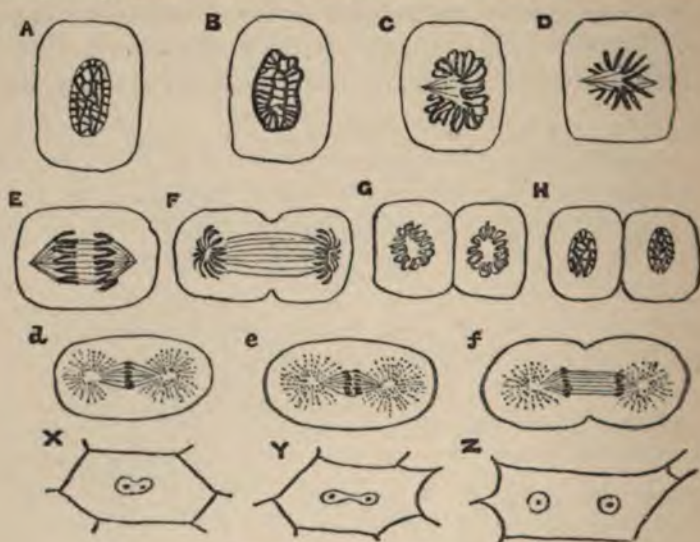


FIG. 13.—NUCLEAR DIVISION.

A-H, karyokinesis of a tissue-cell. A, nuclear reticulum in its ordinary state. B, preparing for division; the contour is less defined, and the fibres thicker and less intricate. C, wreath-stage; the chromatin is arranged in a complicated looping round the equator of the achromatin spindle. D, monaster-stage; the chromatin now appears as centripetal equatorial Vs, each of which should be represented as double. E, a migration of the half of each chromatin loop towards opposite poles of the spindle. F, diaster-stage; the chromatin forms a star round each pole of a spindle, each aster being connected by strands of achromatin. G, daughter wreath-stage; the newly formed nuclei are passing through their retrogressive development, which is completed in the resting-stage, H.

d-f, karyokinesis of an egg-cell, showing the smaller amount of chromatin than in the tissue-cell. The stages d, e, f, correspond to D, E, F, respectively. The polar star at the end of the spindle is composed of protoplasm granules of the cell itself, and must not be mistaken for the diaster (F). The coarse lines represent the chromatin, the fine lines the achromatin, and the dotted lines cell-granules [chiefly modified from Flemming]. X-Z, direct nuclear division in the cells of the embryonic integument of the European Scorpion [after Blochmann].

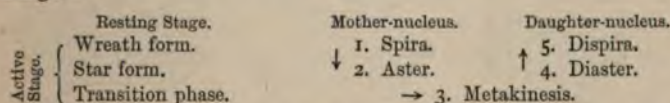
tour becomes less defined, owing to the disappearance of its membrane; the very fine close network appears looser in texture and coarser in fibre; and a contorted looped rosette or wreath of chromatin is eventually formed (fig. 13, A-C). The peripheral loops fracture, leaving a star-like group of V-shaped bars of chromatin (aster or single star), the angles of which point towards the centre. By this time the achromatin has been transformed into a nuclear spindle, and the chromatin wreath and single aster lie at right angles to it in its equatorial plane (C, D). Each bent chromatin bar next divides longitudinally (the division is not shown in the figure), and the loops, instead of pointing inwards, become directed, some towards one pole of the long axis of the nucleus, and some towards the other, forming a double star

or diaster. It is important to remember that each half of every longitudinally split chromatin bar of the single aster travels towards an opposite pole of the spindle to form the daughter-stars (fig. 13, E, F). Thus, the chromatin of every new nucleus is not formed by the simple partition of the parent nuclear network, but by an actual longitudinal splitting of the chromatin fibre itself, by this means ensuring a perfectly equable division, while the preliminary breaking up of the network into bent bars facilitates the process. The daughter-stars thus formed gradually pass through the reverse process, and each, after becoming a wreath, is transformed into a fine reticulum enclosing the achromatin, as in the parent nucleus (fig. 13, G, H).

When the daughter-nuclei are in the stellar stage, the protoplasm of the cell itself becomes constricted, and the cell is usually quite divided by the time the wreath-stage is attained.

This mode of cell-division is known as the "*indirect method*," and the whole process is termed "*karyokinesis*."

The following schema of the phases of indirect cell-division is modified from Flemming:—



Usually, in segmenting oosperms and in many vegetable cells, the chromatin is less abundant, and the achromatin appears to take a larger share in nuclear division than in tissue-cells. At the stage when the chromatin is equatorially situated (the "equatorial plate," which is the equivalent of the wreath and aster stage), the achromatin forms a well-marked spindle-shaped bundle of fibres, the apices of which correspond with the centres of the future nuclei. Later, the chromatin separates into two portions, each of which travels along the achromatin fibres to each apex of the spindle, the diaster stage. The intervening achromatin threads break across the middle and are withdrawn.

Van Beneden, who has most carefully studied these phenomena in the oosperm of *Ascaris*, states that the achromatin spindle is probably always present in the ordinary tissue-cells though difficult of detection; but it is readily visible in egg-cells when they are properly treated with reagents.

During karyokinesis, the granules of the protoplasm of the cell often become radially arranged with regard to the foci of the daughter-nuclei. These alone can be seen in the living egg (fig. 13, d, e, f), and they should not be mistaken for the chromatin fibres, which are only visible after suitable treatment.

The foregoing is a brief summary of the views generally held respecting karyokinesis. Carnoy, however, gives a somewhat different account. As previously mentioned, he finds all cells to be composed of a fine protoplasmic *reticulum* enclosing a fluid *enchylema*, which contains various substances in solution and particles in suspension. The nucleus is similarly constituted, but it possesses in addition a contorted nuclear filament of chromatin. The nuclear reticulum evidently corresponds to the above-mentioned achromatin. According to Carnoy, the convolutions of the nuclear filament very rarely fuse at their intersections so as to constitute an actual network. The wall of nucleus is never formed by the chromatin, but solely at the expense of its reticulum. The latter also forms the nuclear spindle in dividing cells. The polar stars are formed by the reticulum of the cell.

It is probable that there is considerable variation in the method of indirect nuclear division amongst the Metazoa. Very rarely, the nucleus simply divides in half without forming karyolitic figures. This is known as "*direct nuclear division*," and has been observed by Blochmann in the embryonic integument of the European Scorpion, and by Ranvier in the division of leucocytes in Axolotl.

Our present knowledge appears to warrant the following generalisation concerning the evolution of the nucleus. In some of the simplest of all organisms (Protista) no nucleus has yet been observed; probably, however, it will be demonstrated that nucleoplasm (*i.e.*, chromatin) is present in diffused granules, as Gruber has shown is the case in a few Ciliate Infusoria. A concentration of the chromatin occurs in other Protozoa, forming either several small nuclei or a single large one. In most Protozoa the nucleus divides directly, as it may do, though very rarely, amongst the Metazoa. Physiological differentiation has also acted upon the nucleus of Protozoa, and has resulted in great variation in structure and behaviour. In some Heliozoa and Ciliata the nuclear division bears considerable resemblance to the indirect method characteristic of the tissue-cells of Metazoa.

In segmenting oosperms, the process of nuclear division is not so complicated as it is in the tissue-cells of adults—partly owing, perhaps, to a paucity of chromatin;

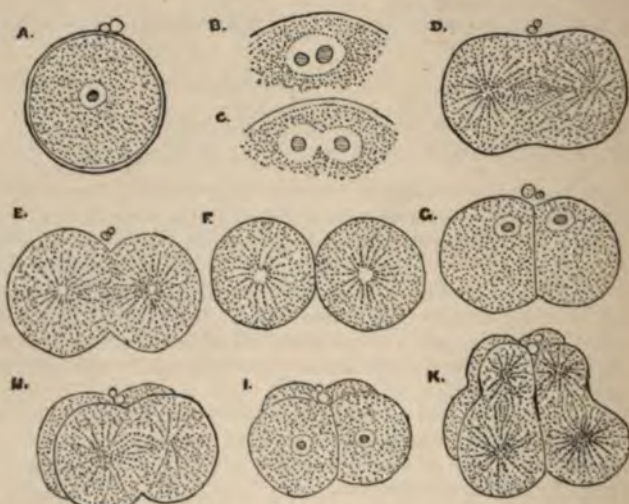


FIG. 14.—EARLY STAGES OF SEGMENTATION OF *ELYSIA VIRIDIS* (drawn from the living egg).

A. oosperm in state of rest after the extrusion of the polar cells; B. the nucleolus alone has divided; C. the nucleus is dividing; D. the nucleus, as such, has disappeared, first segmentation furrow appears; E. later stage; F. oosperm divided into two distinct segmentation spheres—the clear nuclear space in the centre of the aster of granules is growing larger; G. resting-stage of two appressed spheres; H. I. similar stages in the production of four spheres; K. formation of eight-celled stage.

but it is probable that there is an approach in some cases to the direct method of nuclear division which is so common amongst the Protozoa; as, for example, in the segmenting oosperm of *Elysia* (fig. 14, B, C), which may be compared with the nuclear division of the *Amœba* (fig. 1, A-C). This irresistibly suggests a retention by certain segmenting oosperms of the ancestral method of nuclear division.

The segmenting typical oosperm was left at a stage in which two segmentation spheres had been formed.

A second series of changes soon takes place, the long axis of the nuclear spindle lying in the same plane as the first, but at right angles to it; four segmentation-spheres are thus formed, all lying in the same plane (fig. 14, H, I).

After another short resting-stage, each of the four spheres divides in a manner essentially identical with the preceding. As the nuclear spindle assumes a position at right angles to the two previous directions, the third groove is in a horizontal plane, and a mass of eight cells is produced, four above and four below (fig. 14, K). The segmentation has thus taken place in the three dimensions of space.

In the most regular cases of segmentation, the eight spheres are vertically divided to form sixteen spheres, eight above and eight below (fig. 15). In the next stage, a furrow is formed on each side of the first horizontal or equatorial fissure, and these deepen to produce a mass of thirty-two spheres, consisting of four rows of eight cells each. A sixty-four-celled stage is next reached (fig. 15); but usually, after this, the regular rhythm is lost, and the

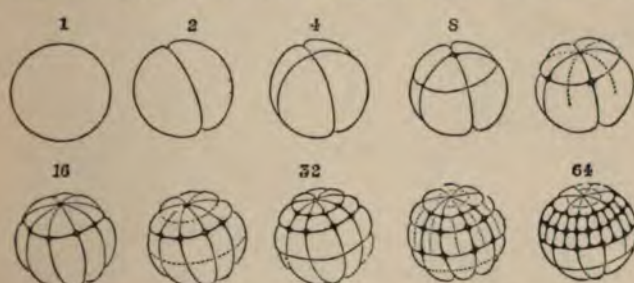


FIG. 15.—SEGMENTATION OF OOSPERM OF FROG. [After Ecker.]

The numbers above the figures refer to the number of segments at that stage. The dotted lines represent the position of the next furrows or planes of segmentation. The segmentation, though regular, is somewhat unequal owing to the presence of yolk.

order of the segmentation becomes obscure. We thus get the number of cells in each successive stage as follows:—A. 1; B. 2; C. 4; D. 8; E. 16; F. 32; G. 64; N. ∞ , that is, in geometrical progression. It must, however, be definitely understood that this is not the invariable rhythm of segmentation, but only a generalised type (for example, the Nudibranchs and other Mollusca do not conform to it).

The result of segmentation is the formation of a multicellular body, usually enclosing a central cavity—"Segmentation cavity" or "*Blastocœl*" (fig. 16, A). The body itself is variously termed "*Blastula*" or "*Blastosphere*." Excepting in special cases, the wall of the Blastula consists of a single layer of cells.

Typical Gastrulation.—An oosperm devoid of food-yolk (known as *alecithal*), or one in which the segmentation is quite

regular, has been assumed, but this rarely obtains; more or less food-yolk is usually present, and its presence is a disturbing factor of great importance. Before, however, discussing the effects of food-yolk upon an oosperm, it will be advisable to continue the history of the simpler condition; the ova of Echinodermata being particularly suitable for this purpose.

On the completion of the Blastula stage, a slight depression occurs at the pole opposite to that where the polar cells are situated. This is often preceded by a flattening of that pole of the

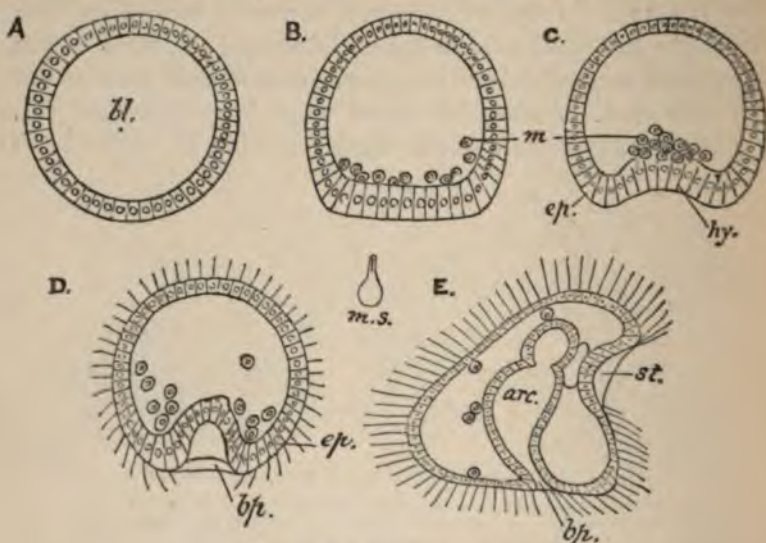


FIG. 16.—GASTRULATION OF ECHINUS.

A. blastula; B. later stage, showing the thickening and flattening of the lower pole and appearance of mesoderm; C. commencement of gastrulation; D. later stage; E. early larval stage with commencing oval invagination; D. and E. from living embryos, after Metschnikoff.
arc. archenteron; bl. blastocoel; bp. blastopore; ep. epiblast; hy. hypoblast; m. mesoblast (mesamoboids); m.s. mesoblast cell secreting a spicule; st. stomodaeum.

blastula (fig. 16, B), the cells of the flattened region assuming a more columnar form, the first indication of a histological differentiation. The invagination deepens until a cup-like cavity is formed (fig. 16, D), and eventually there is usually a complete inversion of this pole of the blastula. The growth of the embryo is so rapid that the size and general form of the body is at first little altered by this process, but soon the absolute size is increased and the embryo becomes oval in shape.

These phenomena result in the formation of a two-layered embryo, which has an orifice at one end, the *Blastopore* or primitive

mouth, opening into a central sac, the cavity of invagination, *Archenteron*, or primitive stomach. The outer layer is the Epiblast (*Ectoderm*), the inner layer lining the archenteron is the Hypoblast (*Endoderm*), and between these layers is a larger or smaller cavity, which is the more or less reduced segmentation cavity. Such an embryo is known as a *Gastrula* (fig. 16, c).

A modification of ordinary invagination is sometimes met with which is worthy of special notice:—In many Nudibranch Mollusca, the blastula is somewhat quadrate in contour and flattened, being not unlike a book in shape (fig. 17). The gastrula is formed by a kind of rolling over, combined with a slight amount of invagination. An elongated blastopore is the result; this closes over from behind forwards, the anterior extremity (as indicated by the polar cells) appearing to persist as the mouth.

An extreme example of the method of gastrula-formation by the rolling round of

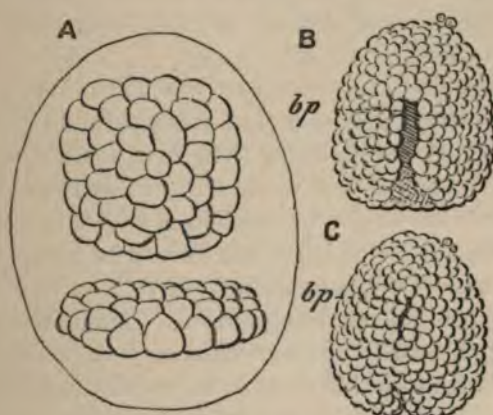


FIG. 17.—GASTRULATION OF *FIONA NOBILIS*.

A. oblong flattened blastula (plakula), two embryos in one egg-shell, the lower one seen endwise; B. gastrula in process of formation; C. gastrula stage—the slit-like blastopore (bp.) will be still further reduced from behind forwards.

a two-layered flat embryo (the *Plakula* of Bütschli) is found in the Nematode Worm, *Cucullanus*. Intermediate stages are, however, to be found in other forms. It will be noticed that in the plakula stage one surface of the embryo is epiblastic, while the other is hypoblastic, and Bütschli compares such an embryo with the problematical organism *Trichoplax adhaerens* [F. E. Schulze].

The effect of food-yolk upon these changes has now to be considered. Though, as previously mentioned, food-yolk is of only secondary significance, yet its presence often greatly influences the manner of segmentation and the early development.

Effect of Food-Yolk, Telolecithal Segmentation.—In the formation of a gastrula by simple invagination, the pole of the oosperm opposite the polar cells ultimately becomes the gastric region of

the embryo. As might be expected, the yolk, which is merely stored-up nutritive material, is usually almost entirely confined to those cells which have a nutritive function, *i.e.*, the hypoblast cells. Ova in which the yolk is especially concentrated at one pole are termed "*telolecithal*." As a matter of fact, it is generally possible to distinguish between the two layers in the blastula before invagination commences—the epiblast cells being smaller and more transparent, while those of the hypoblast are larger, rounder, and more opaque. This distinction is often to be observed at still earlier stages; at the stage of eight segmentation-spheres the four upper cells may be purely epiblastic, while the four lower may be primitive or yolk-hypoblast. According to some investigators, even the *first* furrow may indicate the first epiblastic sphere; but the recent researches of Agassiz and Whitman show this to be very doubtful (see p. 268).

It is not difficult to conceive that the distension of the hypoblast-cells with inert matter would cause them to segment with difficulty, and this would hinder their invagination, while an increase in the amount of yolk would still further retard the process, so that a condition might be reached in which it would be impossible for the distended hypoblast cells to be invaginated at all, and the inertness of the large quantity of yolk would allow of only a very few hypoblast-cells being formed. Though the epiblast has been scarcely affected by the increment of yolk in the lower cells, its behaviour with regard to them is necessarily modified, and since the hypoblast cannot be invaginated, the epiblast is obliged to grow round it (fig. 18, A-D).

One effect, then, of the addition of food-yolk to the ovum is to cause the normal method of gastrula-formation by invagination ("*embolé*") to be modified into that of overgrowth ("*epibolé*"). The segmentation cavity is almost obliterated and the blastopore is greatly reduced, and occasionally may be entirely absent as a distinct orifice (Cephalopoda).

In certain Prosobranch Gastropods, with a large quantity of yolk (*e.g.*, *Ianthina*, *Fusus*), the oosperm divides into two, and again into four, large segmentation-spheres (fig. 18, A and *a*); four small cells are next segmented off from the upper poles of these spheres. There are then, at this stage, four small clear epiblast cells and four large opaque yolk-spheres. The yolk again gives rise to four small cells (fig. 18, B and *b*), and the first four epiblast cells and the four cells just formed themselves divide, so as to

constitute a group of sixteen cells resting upon four large yolk-spheres (fig. 18, c). By further cell-division a cap of small epiblast cells is formed, which gradually extends round the yolk-spheres (fig. 18, c, d, and e), leaving a small uncovered area at the ventral pole, which corresponds to the blastopore of other forms (fig. 18, d and f-bp). The ventral wall of the archenteron (mesenteron of embryo) appears to be formed, or at least partially, by an

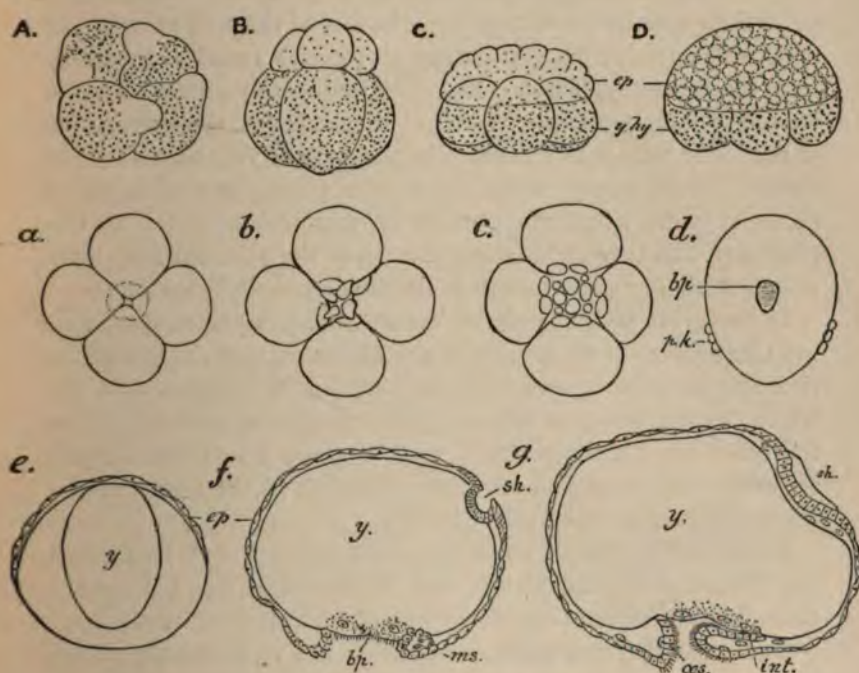


FIG. 18.—SEGMENTATION OF TWO PROSOBRANCHS; to illustrate the effect of the increase of food-yolk.

A-D. *IANTHINA*; the epiblast cells form a cap which gradually grows round the yolk-cells (primitive hypoblast). a-g. *FUSUS* [after Bobretzky]; a-c, surface views from above; d, ventral view; e-g, sections; bp, blastopore; int, commencing intestine; ms, mesoblast; aes, stomodæum; p.k. primitive or larval kidney; sh, shell gland; y, y.h.y. yolk-cells or yolk hypoblast.

ingrowth of cells at the posterior lip of the blastopore; the dorsal wall is certainly produced by the formation of cells (hypoblast) by the yolk-spheres (or primitive hypoblast). The hypoblast cells, especially those situated in the gastric region, actively assimilate the yolk. The blastopore, in some species at least, persists as the mouth, the œsophagus being produced by a further ingrowth of epiblast at that orifice. The segmentation in *Nassa*, as described by Bobretzky, is somewhat different from the above.

The increase in the amount of food-yolk amongst Invertebrates culminates in the Cephalopoda, in which group segmentation results in the formation of a cap of small cells resting upon the large yolk. This yolk may be regarded as one immense lower-layer segmentation-sphere distended with food-yolk, or better, perhaps, as several fused together (primitive hypoblast). The cap of cells is really the epiblast; such a cap or layer of cells (one or more cells deep) resting on the yolk is termed a "*blastoderm*." Soon nuclei make their appearance on the circumference of the yolk at its upper pole, which nuclei, by aggregating protoplasm round themselves, form the future hypoblast cells. This apparently anomalous proceeding is merely a masked form of segmentation, the protoplasm of the lower cells is so enfeebled by the mass of yolk that it cannot divide; but as segmentation must take place, the nuclei, either alone or with a minute portion of protoplasm, travel to the periphery, and there, by the assimilation of the yolk, build up their cells. A similar phenomenon is common amongst Vertebrates.

In two great divisions of the Vermes, the Platyhelminthes and the Chaetopods, do we find, as in the Mollusca, that the segmentation may be more or less uniform, resulting in a hollow blastula, which further develops into a typical invaginate gastrula; or, on the other hand, sufficient yolk may be present to cause unequal segmentation, the partial or total obliteration of the blastocœl and the production of an epibolic gastrula.

Amongst the Platyhelminths, *Lineus* (fig. 49) and *Leptoplana* (fig. 50); and the Earthworm and *Rhynchelmis* (fig. 53) for the *Oligochaeta* illustrate these two types of gastrula formation.

Syncytial Segmentation.—Sedgwick has very recently shown that, even later than the gastrula-stage in the development of the species of *Peripatus* from the Cape of Good Hope, no definite cell-walls are present. The embryo is, in fact, a syncytium (fig. 19). What corresponds to segmentation in other forms is here effected by the multiplication of nuclei, which aggregate round themselves small portions of the continuous vacuolated protoplasm.

The gastrula arises by a process of epibole, and is at first solid. The archenteron (mesenteron) is simply a large vacuole within a multinucleated mass of protoplasm.

It remains to be seen whether the segmentation-spheres in other developing ova are in all cases separate cells, or whether there may not be a direct or indirect protoplasmic continuity between all the cells of an embryo.

There is a considerable resemblance between such an embryo as that given in fig. 19, B, and the parenchymula of *Obelia*, fig. 46, E.

Centrolecithal Segmentation.—The food-yolk is not always concentrated within the future hypoblast cells, since amongst the Arthropoda it is usually equally divided between all the segmentation-spheres, the protoplasm of which is mainly peripherally situated. The passiveness of the yolk, generally, not only prevents any entire segmentation, but causes a separation to take place between the pro-

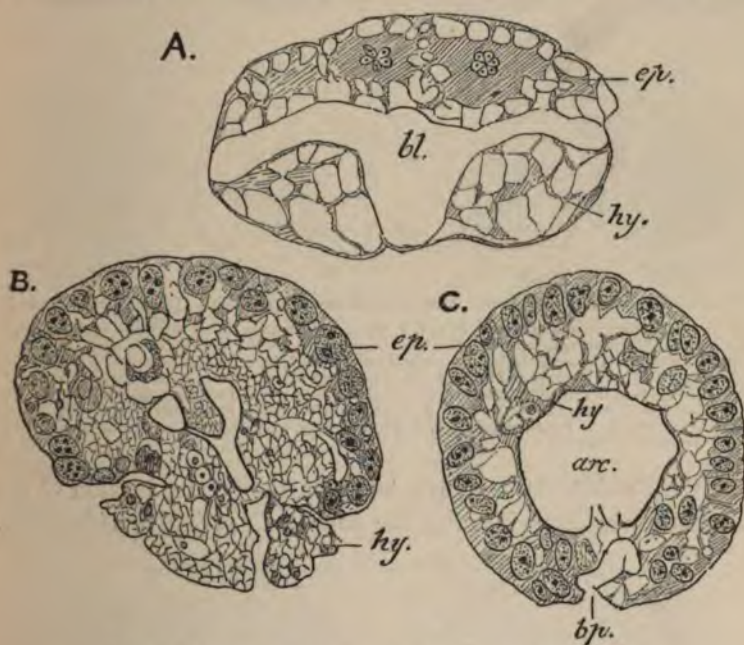


FIG. 19.—SYNCYTIAL SEGMENTATION OF PERIPATUS. [After Sedgwick.]

A. Blastula with about sixteen epiblast cells. B. Early gastrula stage—the central large vacuole is the commencing archenteron. C. Completed gastrula. The whole of the protoplasm is directly continuous and largely vacuolated; the hypoblast is at first non-nucleated.

toplasm and the yolk; thus an external continuous single layer of cells is formed, within which lies a central mass of yolk, more or less free from protoplasm. Such ova are termed "*centrolecithal*."

The details of segmentation vary somewhat in the Crustacea. In such a comparatively simple case as *Callianassa* (fig. 20), the nucleus divides in the ordinary manner, without affecting the yolk, till sixteen nuclei are produced; by this time they have travelled to the periphery of the oosperm, and an external protoplasmic layer is formed, which, on the further multiplication of the nuclei,

becomes divided into distinct cells, thus constituting a shell of cells entirely surrounding a solid core of unsegmented yolk.

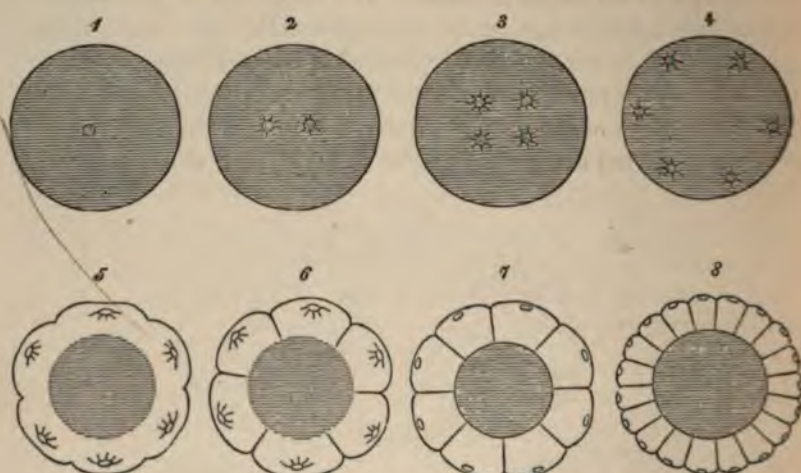


FIG. 20.—SEGMENTATION OF OOSPERM OF *CALLIANASSA SUBTERRANEA*. [After Mereschkowski.]

1-4. The nucleus divides into 2, 4, 8, 16, and the nuclei travel from the centre towards the surface without affecting the oosperm itself. 5-6. 16-cell stage. 5. The oosperm possesses a broad external protoplasmic layer, which passes into the central yolk, the former is raised into slight prominences, which correspond to the underlying nuclei; in 6 the different cells are segmented off from one another, but not from the central yolk. 7. Further cell-division has occurred, and the cells are cut off from the yolk. 8. A single-layered blastoderm of columnar cells surrounds the yolk.

In the Fresh-water Crayfish, however, the greater portion of the yolk itself segments, forming the so-called "yolk-pyramids" (figs.

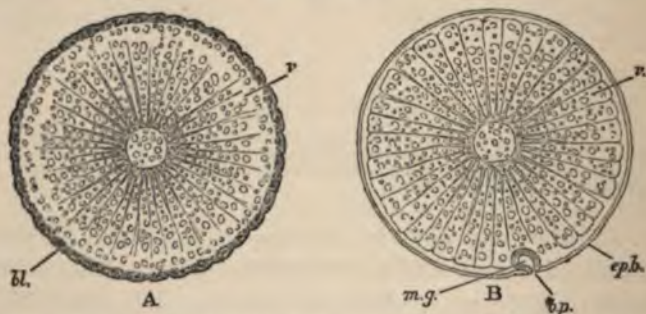


FIG. 21.—BLASTULA AND GASTRULA OF FRESH-WATER CRAYFISH (*ASTACUS FLUVIATILIS*). [After Reichenbach and Huxley.]

A. Ovum with the blastoderm, *bl.*, not yet separated from the imperfectly segmented yolk, *v.* B. Ovum in which the epiblast, *ep.b.*, is completely separated from the yolk, and the archenteric invagination to form the mid-gut or mesenteron, *m.g.*, has taken place, *b.p.*, blastopore.

21 and 22, A). Subsequently the nucleated peripheral portion of each segment breaks away from the yolk-pyramids (fig. 21, B);

and although the latter retain their segmentation for a long time, they are not to be regarded as having the value of cells, but are merely masses of non-nucleated yolk, with little, if any, active protoplasm.

Amongst the Crustacea, invagination takes place at one pole of the blastula and a gastrula is formed, the residual yolk being of necessity contained within the segmentation-cavity. The yolk is gradually absorbed by the hypoblast cells, which emit pseudopodial processes for that purpose (fig. 22, E, *p*). Thus the primitively



FIG. 22.—FIGURES ILLUSTRATING THE DEVELOPMENT OF *ASTACUS*.
[From T. J. Parker after Reichenbach.]

A. Section through part of oosperm during segmentation. B and C. Longitudinal sections during the gastrula stage. D. Highly magnified view of the anterior lip of blastopore to show the origin of the primary mesoblast from the wall of the archenteron. E. Two hypoblast-cells to show the intra-cellular digestion of yolk spheres. F. Hypoblast-cells giving rise endogenously to the secondary mesoblast.
a. Archenteron; *b.* blastopore; *c.* central yolk mass; *ec.* epiblast; *en.* hypoblast; *n.* nuclei; *p.* pseudopodial process; *p.ms.* primary mesoblast; *s.ms.* secondary mesoblast; *w.y.* white yolk; *y.* yolk granules; *y.p.* yolk pyramids.

small hypoblast cells become greatly distended with yolk. This is what occurs in the Crayfish, and with variations is characteristic of the Crustacea.

The peculiar segmentation of most Insects may be regarded as an extreme modification of the Crustacean type.

B. Chordata—Alecithal Segmentation.—The egg of *Amphioxus* having very little food-yolk, undergoes entire and regular segmentation up to the stage of thirty-two spheres. The segmentation then becomes slightly irregular, but results in an almost

spherical blastula, the cells of the lower pole of which are slightly larger than the remainder. This pole flattens (fig. 23, A) and invaginates to form a wide-mouthed gastrula, in which the segmentation cavity is obliterated (fig. 23, C). The blastopore narrows to a small orifice, and the epiblast becomes ciliated. The gastrula elongates and its dorsal side becomes flattened. Thus the blastopore comes to have a dorso-terminal position (fig. 57, D). A pair of "hinder-pole mesoderm cells" early make their appearance on the future ventral side of the lip of the blastopore; their further history is noticed later (p. 61).

Effect of Increase of Food-Yolk.—In the Chordata, as in most Invertebrates, the yolk is stored up in the lower portion of the oosperm, and it is consequently contained within the segmentation-spheres of that pole—in other words, within the hypoblast. These



FIG. 23.—BLASTULA AND GASTRULA OF AMPHIOXUS. [From Claus after Hatschek.]

A. Blastula with flattened lower pole of larger cells. B. Commencing invagination. C. Gastrulation completed; the blastopore is still widely open, and one of the two hinder-pole mesoderm cells is seen at its ventral lip. The cilia of the epiblast cells are not represented.

cells usually have a somewhat complicated history, especially when greatly charged with yolk; as the primitive hypoblast in that case is only partially concerned in the formation of the digestive tract of the future embryo, it is sometimes termed yolk-hypoblast or lower-layer cells, to distinguish it from the hypoblast of the adult.

The effect of the increase of yolk in the vertebrate oosperm on segmentation and gastrulation resembles in the main that which occurs in some Molluscs. The segmentation is unequal, and the blastocoel is reduced in extent. The epiblast grows round the enlarged hypoblast, and consequently the gastrulation is asymmetrical. The invagination of the hypoblast is but partial, and tends to be increasingly reduced. The primitive blastopore of the true gastrula stage is more and more filled up by yolk-cells (the yolk

plug, fig. 24), and it becomes almost if not entirely obliterated as an actual orifice.

The epiblast usually at first consists of a single layer of cells, and its history is simple.

During gastrulation a definite ingrowth of hypoblast occurs at the dorsal lip of the blastopore. This is most marked in forms where there is but a small amount of yolk, and least so in ova with a great deal of yolk. This hypoblast is sometimes spoken of as invaginated hypoblast—or, better, axial hypoblast, as it extends along the median line of the roof of the archenteron. As this tissue gives rise to the notochord, it is called by Hertwig and others *Chorda-entoblast* (see figs. 59–64, *ax. hy.*)

The sides and floor of the archenteron are bounded by the yolk-cells in forms which have a relatively small amount of yolk. In these ova the yolk cells which immediately bound the archenteron are usually directly transformed into the definite hypoblast of the digestive portion of the alimentary canal or mesenteron. These cells may be called the digestive or gut-hypoblast, or simply hypoblast; this is the *Darm-entoblast* of the Germans (figs. 60–65, *hy.*). These cells are distinctly different in character from the axial hypoblast. In forms with a great deal of food yolk these cells have a slightly different origin, as will be shortly described.

The remaining yolk-cells may be termed the yolk-hypoblast; and, like the unsegmented yolk, they simply serve as pabulum for the developing embryo.

In telolecithal ova with a large amount of yolk, only a small cap of primitive hypoblast-cells is formed; in this case these are usually termed lower-layer cells. These lower-layer cells more or less entirely surround the segmentation cavity, and themselves rest upon the large unsegmented yolk (figs. 25, 26, 31).

The segmentation cavity or blastocoel in all alecithal ova is bounded on the one hand by the epiblast and on the other by the hypoblast (figs. 16, 19, 23, 24). Even in such an extreme telolecithal type as the Bird, Duval has shown that the same condition obtains in a very early stage (fig. 29). Thus the encroachment of the lower-layer cells round the segmentation cavity in the Elasmobranchs (fig. 26) is a purely secondary condition of no special import.

As will be described in its appropriate place, the primitive hypoblast also gives rise to the main mass of the mesoblast. It is convenient to restrict the name of archenteron to the cavity of the early gastrula stage, and after the formation of the mesoblast to term the corresponding cavity the mesenteron (that is, the hypo-

blastic portion of the alimentary canal comprising the pharynx, œsophagus, stomach, and intestine). The reasons for this will presently appear sufficiently obvious.

The effects of the gradual increase of food-yolk in oosperms will now be illustrated in more detail.

In the Lamprey (figs. 60, 61), and slightly more so in the Newt (figs. 58, 59), enough yolk is present to cause the cells of the primitive hypoblast to be larger than those of the epiblast, and to induce an asymmetrical invagination. The axial hypoblast

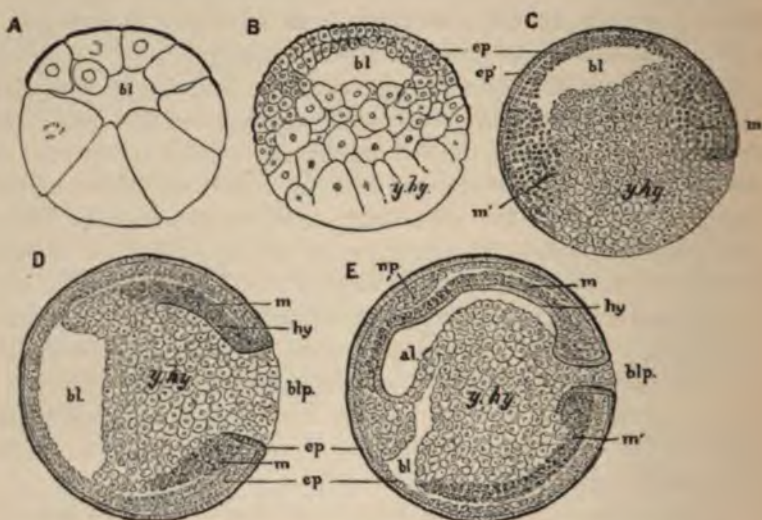


FIG. 24.—BLASTULA AND GASTRULA STAGES OF THE FROG (*Rana temporaria*).
[After Götte.]

A. early blastula stage; B. late blastula; C. commencing gastrula; D. later stage; E. completed gastrula stage, longitudinal section to one side of the median line.
al. archenteron (mesenteron); bl. blastocoel; bl.p. blastopore; ep. deeper, and ep', epidermal layer of epiblast; hy. hypoblast; m. dorsal, and m'. ventral mesoblast; n.p. neural plate of future brain; y.hy. yolk hypoblast.

is very distinct, and the yolk-cells forming the sides and floor of the archenteron are transformed into the hypoblast of the mesenteron.

More yolk is present in the Frog's oosperm, but the first stages of segmentation are only slightly affected by this increase. The third furrow, instead of being equatorial, is nearer to the upper or black pole of the egg (figs. 15 and 24): as this pole is less burdened with yolk than the lower pole, it is only to be expected that segmentation should be more rapid and complete there. In the

final blastula stage, the segmentation-cavity is bounded above by two layers of epiblast, an epidermal and an inner nervous layer, the latter eventually becoming three cells thick.

The epiblast gradually extends over the surface of the primitive hypoblast and the uncovered portion (yolk-plug, anus of Rusconi) is reduced to a small round white spot, entirely surrounded by the darkly pigmented epiblast (fig. 24, *blp*). The posterior extremity of the future embryo is formed by the dorsal lip of the blastopore. At this point an ingrowth of cells occurs (fig. 24, *D. hy*), which constitutes the hypoblastic dorsal wall of the mesenteron. The ingrowth of the hypoblast continues, and a slit-like archenteron appears between it and the yolk hypoblast. Meanwhile the segmentation-cavity has been pushed to one side, and eventually disappears. The gastrula in the Frog is thus formed partly by invagination (*embolé*), partly by overgrowth (*epibolé*).

In some forms (*e.g.*, Sturgeon) the primitive hypoblast extends up the sides of the segmentation-cavity and helps to form its roof.

Given more yolk, further complications would arise. Balfour has drawn an ideal type (fig. 25), intended to illustrate the passage from the Amphibian to the Elasmobranch gastrula. The segmentation-cavity is entirely surrounded by lower-layer cells, and below these again is the unsegmented yolk penetrated by a protoplasmic reticulum. This is merely an exaggeration of the tendency to a separation which occurs in the primitive hypoblast between cells containing less from those containing more yolk. On reference to the Frog's ovum in fig. 24, *C*, a mass of smaller primitive hypoblast cells (*m*) will be seen at the lips of the blastopore, which corresponds to the cap of lower-layer cells of fig. 25, *A*.

Asymmetrical invagination is assumed to occur in this ideal type, the invaginated hypoblast forming the roof of the archenteron, while a portion at least of its floor is derived from cells which form round those scattered nuclei (fig. 25, *B*, *n*) which appear below the archenteron, and which are themselves derived from the nuclei of the primitive yolk-cells.

Telolecithal Segmentation and Gastrulation.—Owing to the immense amount of yolk in the oosperm of an Elasmobranch, segmentation is only very partial. The protoplasm of the oosperm mainly segregates to the upper pole, and here also the yolk granules are of smaller size: this area is termed the germinal disc. A delicate protoplasmic network extends throughout the whole of the yolk.

Segmentation commences by a groove extending nearly across the germinal disc; this is crossed by a second at right angles to it; subsequently other grooves appear, and horizontal fissures convert these into polygonal masses, each of which is provided with a nucleus, and is, in fact, a segmentation sphere (compare fig. 27). Eventually a circular cap (blastoderm) of minute cells is formed,

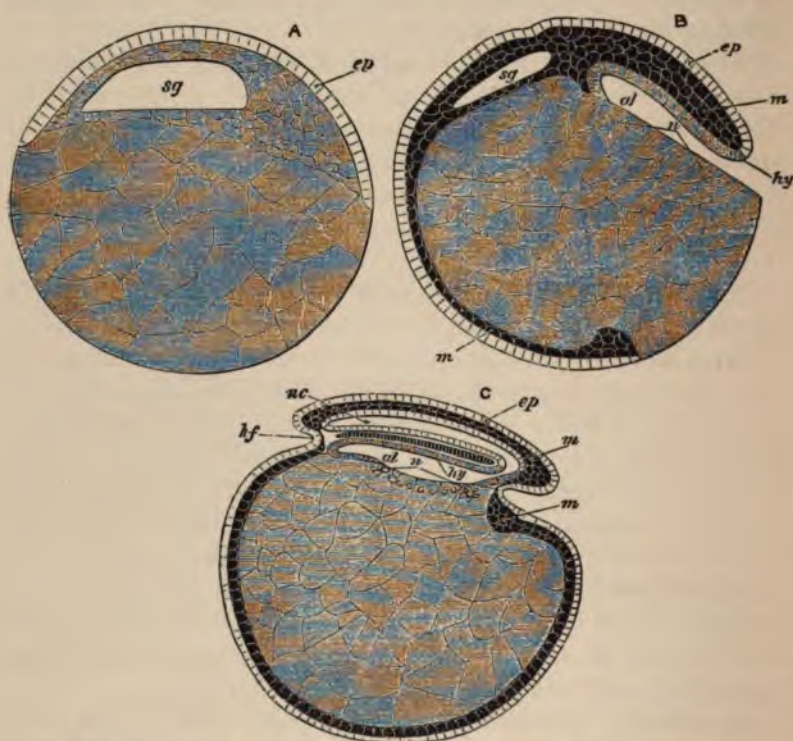


FIG. 25.—THREE DIAGRAMMATIC LONGITUDINAL SECTIONS THROUGH AN IDEAL TYPE OF VERTEBRATE EMBRYO, INTERMEDIATE IN THE MODE OF FORMATION OF ITS LAYERS BETWEEN AMPHIBIA OR LAMPREY AND ELASMOBRANCHII. [From Balfour.]

al. mid-gut; ep. epiblast; hf. head-fold; hy. hypoblast; m. mesoblast; n. nuclei of the yolk; nc. neural canal; sg. segmentation-cavity.

of which an upper layer is distinctly columnar and constitutes the epiblast, while the underlying mass of rounded or polygonal cells is the primitive hypoblast or lower-layer cells. A cavity, the segmentation-cavity, soon occurs within the latter. Although the blastoderm is sharply defined from the underlying yolk, the latter must be regarded as essentially homologous with the lower-layer cells, the main difference being that the primitive hypoblast

segments into definite cells in that area where there is sufficient protoplasm, whereas in the greater portion of its mass it is unable to segment, owing to the preponderance of food-yolk. Nevertheless, the nuclei belonging to the latter divide, and the nuclei thus produced (figs. 25, B, C, 26, *n*) may be seen at the upper surface of the so-called yolk. In process of time these free nuclei form cells, of which some pass into the blastoderm, and others will constitute the floor of the mesenteron.

At one region the blastoderm projects slightly from the yolk, forming what is termed the embryonic rim. At this spot the epiblast, bending round the rim, imperceptibly passes into a columnar layer (hypoblast proper), which is being differentiated from the lower-layer cells (fig. 26). This differentiation extends anteriorly,



FIG. 26.—LONGITUDINAL SECTION THROUGH THE BLASTODERM OF AN ELASMOBRANCH DURING GASTRULATION. [Modified from Balfour.]

a. archenteron (mesenteron); *e.r.* embryonic rim; *ep.* epiblast; *hy.* hypoblast—the line points to the spot where the invagination occurs at the dorsal rim of the blastopore; *l.l.* lower-layer cells or primitive hypoblast; *m.* mesoblast; *n.* nuclei of the yolk; *s.c.* segmentation cavity.

In the corner a nucleus of the yolk is shown very highly magnified, and a portion of the protoplasmic network connected with the nucleus.

and a space is left between the developing hypoblast and the underlying yolk. The embryonic rim is the dorsal lip of the blastopore; the anteriorly progressive differentiation of the lower-layer cells into true hypoblast corresponds with the gastrula invagination of other types, and the cavity between the hypoblast and the yolk is the archenteron or the future mesenteron. Those lower-layer cells which do not participate in the hypoblast constitute the mesoblast (see p. 67).

The blastopore proper is situated at the posterior end of the embryo. The blastoderm gradually extends over the yolk in every direction except immediately behind the embryo, which thus comes to be situated at the end of a bay or sinus. In process of time the yolk is entirely surrounded by the blastoderm, the edges of which unite in a linear manner (primitive streak) behind the embryo (fig. 35, B, *bl*).

The segmentation of the Fowl's egg corresponds sufficiently closely with that of an Elasmobranch to obviate a description. Fig. 27 illustrates a superficial view of the segmenting blastoderm, and figs. 28-31 show sections at various stages of segmentation. Duval states that the segmentation-cavity appears very early (fig. 29); it is bounded above by a single layer of epiblast-cells, and at first below by a single layer of primitive hypoblast cells;

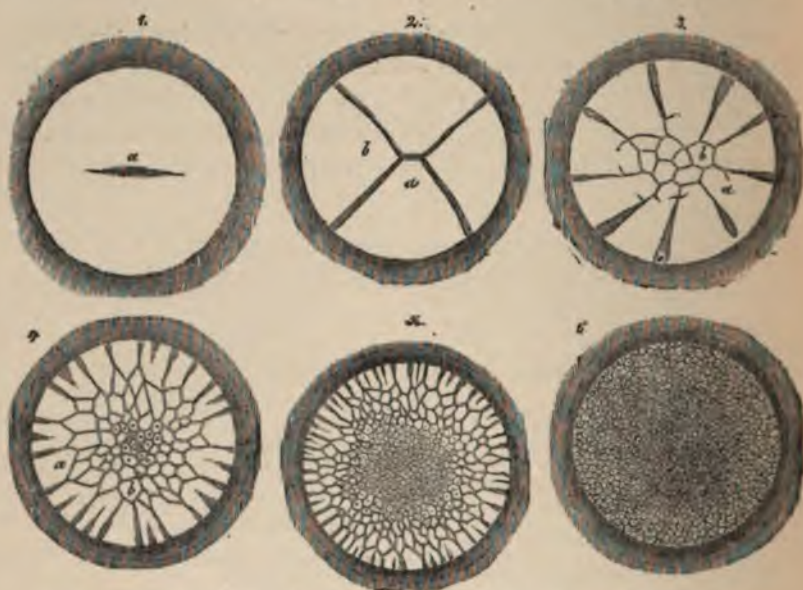


FIG. 27.—SURFACE VIEWS OF SIX STAGES IN THE SEGMENTATION OF A FOWL'S OOSPERM.
[From Kolliker after Coste.]

All the eggs were taken from the lower portion of the oviduct. The shading outside the germinal disc represents the yolk. Diameter of the germinal disc, 3 mm.

1. Earliest stage; *a*, the first furrow. 2. Stage of four imperfect cells separated by furrows. 3. Stage of nine meridian furrows and cross-furrows have also appeared, which divide the disc into nine large peripheral cells and seven small central cells. 4. A later stage nuclei are to be seen in the central clearer cells; the cells are polygonal through mutual pressure. 5. Further stage in segmentation; the cells gradually decrease in size towards the centre. 6. Completion of segmentation; the blastoderm consists of an upper layer of small cubical cells (epiblast) and a lower-layer mass of larger cells.

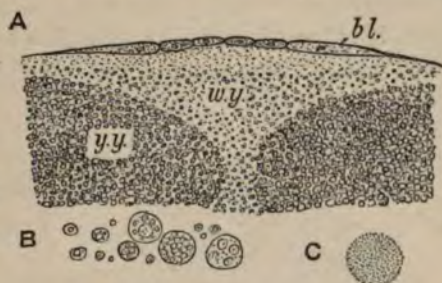
but the latter soon becomes composed of several layers and the segmentation-cavity is obliterated. The blastoderm of a newly-laid egg (figs. 30 and 31) consists of a definite epiblastic layer and an inferior irregular mass of rounded cells, the primitive hypoblast (lower-layer cells), which lies loosely on the yolk. In the upper surface of the yolk free nuclei occur, which have the same significance as those of the Elasmobranch ovum, *i.e.*, they represent primitive hypoblast cells whose walls are not limited. After incu-

bating for an hour or two the latter mass is differentiated into a lower stratum of flattened cells, the hypoblast proper, and scattered mesoblast cells lying between the epiblast and hypoblast. The

FIG. 28. — SEMI-DIAGRAMMATIC SECTION THROUGH A FOWL'S BLASTODERM CORRESPONDING TO NO. 3, FIG. 27. [Modified from Kolliker and Bal-four.]

B. white yolk spheres; C. isolated yellow yolk-sphere.
bl. blastoderm; w.y. white yolk, the upper finely granular layer of which is the seat of cell-formation; y.y. yellow yolk.

Fig. A. is cut off just where the white yolk is expanding to form the central mass.

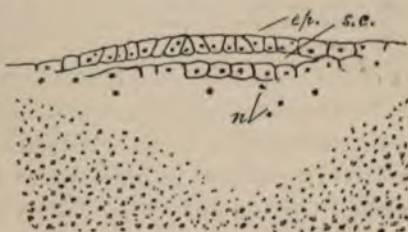


imperfect cavity (sub-germinal cavity) between the hypoblast and yolk corresponds with the archenteron of other forms.

Duval has figured a longitudinal section of the blastoderm of a

FIG. 29. — SECTION THROUGH THE BLASTODERM OF AN UNFERTILISED NEWLY-LAID FOWL'S OVUM IN THE BLASTULA STAGE. [After Duval.]

ep. epiblast; n. free nuclei in the yolk, which aggregate protoplasm round themselves to form primitive hypoblast cells; s.c. segmentation-cavity (blastocoel). The white yolk is left blank; it rests upon the coarser yellow yolk, represented by dots.



Canary about this stage (fig. 32). The slit between the blastoderm and the yolk is at the posterior end of the future embryo, and corresponds with the slit-like archenteric invagination of the Lamprey

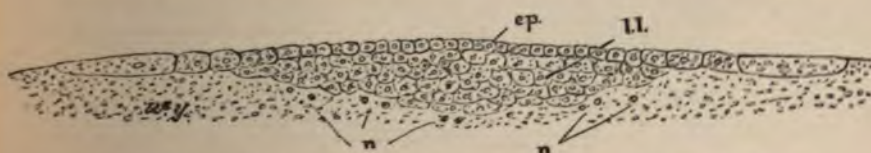


FIG. 30. — SEMI-DIAGRAMMATIC SECTION THROUGH THE GERMINAL DISC OF A FOWL DURING THE LATER STAGES OF SEGMENTATION.

The central cells are the smallest owing to rapid segmentation; the large peripheral cells of the epiblast rest directly upon the white yolk; ep. epiblast; ll. primitive hypoblast; n. free nuclei in the yolk; w.y. white yolk.

(fig. 60) or Frog (fig. 24), or better still, with stage B, or one somewhat earlier, of the diagram of the ideal vertebrate (fig. 25). The yolk of the Bird is clearly homologous with the yolk-cells of the Frog; and the surface of the yolk uncovered by the blastoderm

of the one corresponds with that area of the yolk-cells not surrounded by the epiblast in the other.

It must be remembered that the blastoderm at this stage covers only a very small extent of the surface of the ovum, and that figures so greatly enlarged as figs. 30-32 rather tend to give an exaggerated idea of the relative size of the blastoderm with regard to the

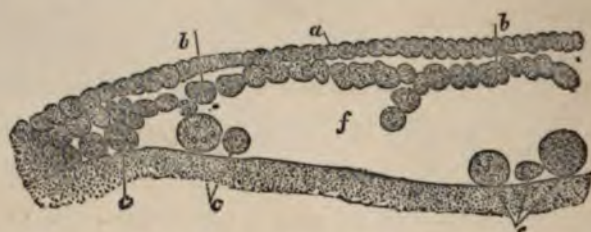


FIG. 31.—PORTION OF A SECTION THROUGH AN UNINCUBATED FOWL'S OOSPERM. [From Klein.]

The thin upper layer *a*. (epiblast) is composed of a single layer of columnar cells; at the edge it rests directly upon the white yolk; *b*, irregularly disposed lower-layer cells (primitive hypoblast); *c*, the larger so-called formative cells resting on the white yolk; *f*, archenteron; the segmentation-cavity is the nearly obliterated space between the epiblast and hypoblast.

rest of the oosperm. The blastoderm of this stage is considerably smaller than the central pale area in fig. 6.

In a surface view of the blastoderm of a newly laid Fowl's egg, a central transparent nearly circular space (area pellucida) is seen surrounded by an opaque ring (area opaca). The former appearance is due to the fact that the blastoderm is separated from the yolk by a shallow space filled with a fluid, whereas the area opaca



FIG. 32.—SECTION THROUGH THE BLASTODERM OF AN UNFERTILIZED CANARY'S OVUM IN THE GASTRULA STAGE. [After Duval.]

Bp., blastopore; *ep.*, epiblast, below which is the primitive hypoblast or lower-layer cells; *n.*, free nuclei, which will form primitive hypoblast cells.

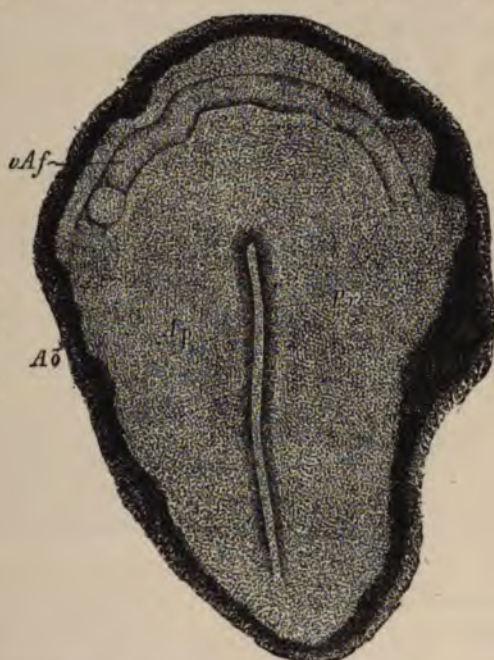
rests on the yolk itself. The embryo is developed within the area pellucida alone (see fig. 6). The area opaca gradually extends over the whole surface of the ovum enclosing the yolk, its lower-layer of primitive hypoblast gradually assimilates the enclosed yolk. That portion of the area opaca immediately surrounding the area pellucida develops a large number of blood-vessels and is known as the area vasculosa. Nutritive matter is transmitted

to the blood by the hypoblast of the area opaca, and by it conveyed to all the regions of the body of the embryo.

To anticipate, as the embryo is being formed, an anterior, and later a posterior, fold in the blastoderm make their appearance, which mark the anterior and posterior extremities of the embryo; they are known as the head and tail folds. The head-fold travels backwards and the tail-fold forwards in such a manner as to constrict the embryo from off the yolk. Less marked lateral folds also appear. Eventually the embryo is quite constricted off the yolk, so that it is merely connected with the latter (or yolk-sac, as

FIG. 33.—SURFACE VIEW OF THE PELLUCID AREA OF THE BLASTODERM OF A FOWL OF TWENTY HOURS. Magnified 24 diameters. [From Kölliker after His.]

AO, area opaca; *Ap*, area pellucida; *Pr*, primitive streak; *vAf*, head-fold.



it is now termed) by a narrow stalk. The development of the embryonic structures known as the amnion and the allantois will be considered in another section (p. 78).

The Primitive Streak.—The first noticeable sign of incubation in the blastoderm of the Amniota when viewed from above is the appearance of an opaque band which extends some distance forwards from the posterior margin of the area pellucida. This is the primitive streak, and its opacity is due to the presence of a greater thickness of cells than occurs elsewhere. Shortly after the primitive streak is formed a shallow groove (the primitive groove)

extends along its whole length. The area pellucida soon becomes oval in outline, and the primitive streak assumes a more central position (fig. 33).

In a transverse section through the primitive streak on its first appearance, the blastoderm is seen to consist of an external layer of columnar epiblast; inferiorly there is a layer of flattened cells (hypoblast) which extends from one yolk-wall to the other. Between those two layers is the third germinal layer or mesoblast. On each side, especially close to the yolk or germinal wall, the mesoblast cells are loosely heaped up, whereas in the centre they form a dense mass, which, appearing through the epiblast, gives its characteristic appearance to the primitive streak. In the region of the primitive streak a fusion of the epiblast with the axial



FIG. 34.—TRANSVERSE SECTION THROUGH THE ANTERIOR END OF THE PRIMITIVE STREAK OF A FOWL'S BLASTODERM ABOUT THE AGE OF FIG. 34. [From Balfour.]

Showing the rounded mesoblast cells arising from the primitive streak and the stellate cells of hypoblastic origin.
ep. epiblast; hy. hypoblast; m. mesoblast; pr. primitive groove; yh. yolk of germinal wall.

mesoblast always occurs (figs. 34, 43), and a complete fusion of all the layers occurs in a limited area in some forms (fig. 43, c).

At a slightly later stage, on the appearance of the primitive groove, the epiblast and hypoblast have much the same character as before. The axial or primitive-streak mesoblast has, however, a greater lateral extension (fig. 34), and is readily distinguishable from the other mesoblastic cells, which have now assumed a stellate character.

Although, for the sake of convenience, an account of the formation of the mesoblast is relegated to another chapter, it is impossible to avoid referring to this germinal layer in this place, as its history is so closely connected with that of the primitive streak.

The changes which have occurred are briefly these. The lower-layer cells or primitive hypoblast have become differentiated into an inferior sheet of flattened cells (hypoblast) and an intermediate tissue of scattered cells (mesoblast). In the mesial line behind the future embryo, the epiblast by rapid cell-division (proliferation) has given rise to a linear mass of axial mesoblast, which later widens out into a lateral sheet of cells.

Nature of the Primitive Streak.—Very much has been written concerning the significance of the primitive streak, but it

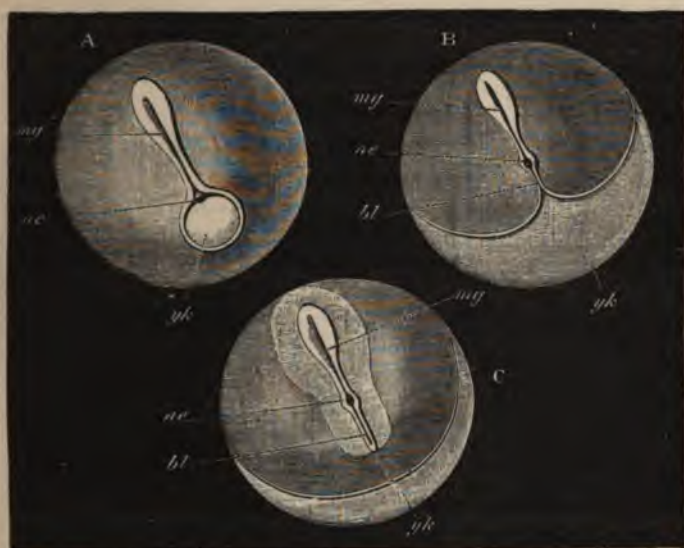


FIG. 35.—DIAGRAMS ILLUSTRATING THE POSITION OF THE BLASTOPORE, AND THE RELATION OF THE EMBRYO TO THE YOLK IN VARIOUS MEROBLASTIC VERTEBRATE OOSPERMS.

A. Type of Frog. B. Elasmobranch type. C. Amniotic Vertebrate. [From Balfour.]

bl. primitive streak, caused by concrescence of the lips of the blastoderm behind the embryo; mg. medullary or neural groove in the centre of the neural plate; ne. blastopore; yk. part of the yolk not yet enclosed by the blastoderm.

is now generally admitted that it represents the fusion of the lips of the blastoderm, which meet behind the blastopore.

The embryo develops subsequently in front of the primitive streak, the posterior end of the one coinciding with the anterior end of the other (figs. 100, 101). At the anterior end of the primitive streak a pit usually occurs, which frequently perforates the blastoderm, and corresponds to the blastopore. In the Lizard, Weldon finds that the primitive hypoblast first takes on the character of the permanent hypoblast at the anterior border of this

pit (blastopore), in this respect recalling the development of the so-called invaginated hypoblast of an Elasmobranch. In the primitive streak of a Lizard all the three layers are fused together.

Fig. 35 graphically illustrates how Balfour assumes the primitive streak to have originated. Fig. A represents a view of a Frog's oosperm at a slightly later stage than Fig. 62; the yolk-cells are still slightly uncovered. An Elasmobranch's oosperm is shown at B; owing to the large increase in the yolk the latter is largely uncovered, but the blastoderm gradually fuses in the middle line behind the



FIG. 36.—PORTION OF THE BLASTODERM OF AN ABNORMAL FOWL'S OVUM OF EIGHTEEN HOURS' INCUBATION. [After Whitman.]

a.o. area opaca, a small portion of which has alone been shaded; a.p. area pellucida; p.g. primitive groove; p.p.g. posterior prolongation of primitive groove; p.s. primitive streak; m.n. marginal notch.

posterior end of the embryo, so that the latter comes to be centrally situated in the blastoderm. By an abbreviation of this process in the Sauropsida, the primitive streak itself is developed towards the centre of the blastoderm (fig. 35, c). This diagram indicates the area pellucida with the developing embryo surrounded by the area opaca, and beyond this again is the uncovered yolk. The edge of the area opaca is often notched immediately opposite to the posterior end of the primitive streak; and Whitman has described an abnormal form of a Fowl's blastoderm (fig. 36) in which the primitive streak extended right across the area opaca

to the marginal notch, which is plainly a reversion to a stage analogous to that figured in fig. 35, B.

Since the epiblast becomes continuous with the primitive hypoblast at the lips of the blastopore of the Frog, it follows that on the junction of such lips there would be a fusion of the layers :

FIG. 37.—SECTION THROUGH THE YOLK-BLASTOPORE OF OOSPERM OF NIGHTINGALE. [After Duval.]

ep. epiblast; hy. hypoblast; m. mesoblast; y. yolk, forming a yolk-plug in the blastopore.



this actually occurs in the Lizard. If a differentiation previously took place between the mesoblast and permanent hypoblast, the fusion of the layers would be less evident. It is then not surprising that, in such an abbreviated development of the primitive streak as we find in the Fowl, the hypoblast is already separated as a distinct layer (fig. 34). A comparison of a transverse sec-

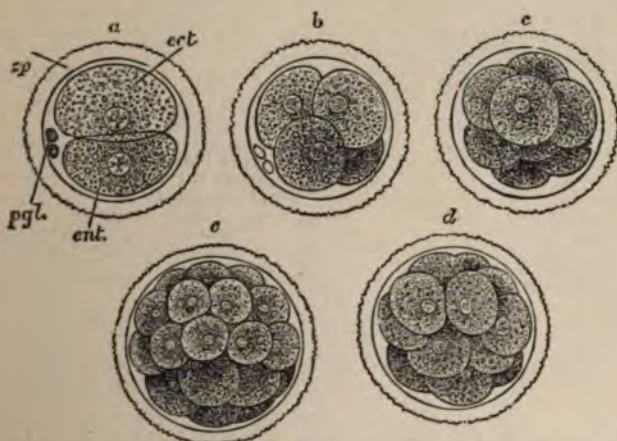


FIG. 38.—FIRST STAGES OF SEGMENTATION OF A RABBIT'S OOSPERM: SEMI-DIAGRAMMATIC. [From Quain; drawn by Allen Thomson after E. Van Beneden's description.]

a. two-cell stage; b. four-cell stage; c. eight-cell stage; d, e. later stages of segmentation, showing the more rapid division of the outer-layer cells and the enclosure of the inner-layer cells; ect. outer-layer cells; ent. inner-layer cells; pgl. polar cells; sp. zona pellucida.

tion of an uncoalesced primitive streak of a Nightingale (fig. 37) with the almost completed blastopore of a Frog (fig. 62, c, and d) will further tend to demonstrate the complete homology of the two stages. Duval has found traces of a similar condition in some Fowls' eggs, and the same may also be seen in a transverse section

of the blastopore of a Lizard. Mitsukuri and Ishikawa have very recently described a perfectly similar stage in the Turtle (*Trionyx*).

Segmentation of the Mammalian Oosperm—Blastodermic Vesicle.—So far as is known, the oosperm of all the higher Mammals (*Eutheria*) undergo total and, at first, regular segmentation. In the Rabbit, according to Van Beneden, the first furrow separates what he terms the epiblast from the hypoblast; but it will be better, for the present, to call them, with Heape, the outer and

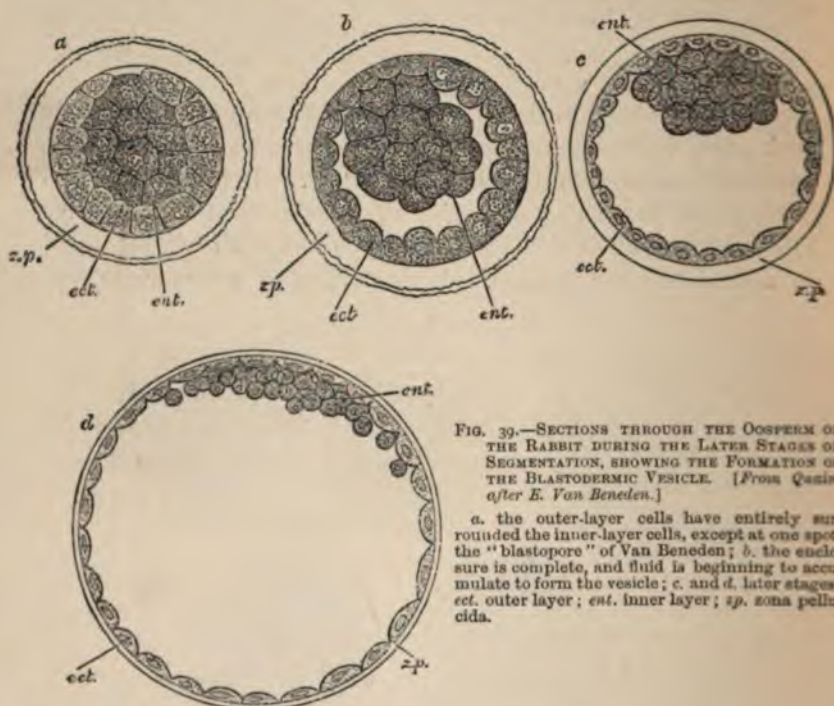


FIG. 39.—SECTIONS THROUGH THE OOSPERM OF THE RABBIT DURING THE LATER STAGES OF SEGMENTATION, SHOWING THE FORMATION OF THE BLASTODERMIC VESICLE. [From *Quina*, after E. Van Beneden.]

a. the outer-layer cells have entirely surrounded the inner-layer cells, except at one spot, the "blastopore" of Van Beneden; b. the enclosure is complete, and fluid is beginning to accumulate to form the vesicle; c. and d. later stages; ect. outer layer; ent. inner layer; z.p. zona pellucida.

inner layer cells (fig. 38). Each sphere divides into two, and these into two more spheres.

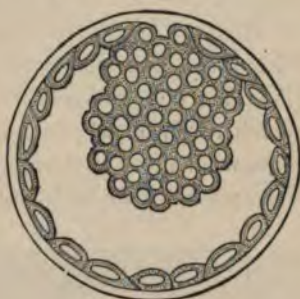
In the eight-celled stage (fig. 38, c) one inner-layer cell is more centrally situated. Further segmentation results in a cap of smaller, more transparent outer-layer cells surrounding a solid mass of granular inner-layer cells (fig. 38, e). Eventually the latter are entirely surrounded, except at one spot, the so-called "blastopore" of Van Beneden (fig. 39, a), but this is also rapidly closed over.

The outer layer next enlarges so as to form what is termed the

blastodermic vesicle, while the inner layer remains attached as an irregular mass to that pole of the ovum where Van Beneden's "blastopore" was situated. Later the blastodermic vesicle increases in size, and is bounded by a single layer of flattened outer-layer cells, and the inner layer forms a small disc of cells attached to the upper side of the vesicle (fig. 39, *d*). In the Bat, however, the "blastopore" of Van Beneden is larger, and persists until there is a considerable cavity in the blastodermic vesicle (fig. 40).

FIG. 40.—SECTION THROUGH THE BLASTODERMIC VESICLE OF A BAT. [After Van Beneden and Julia.]

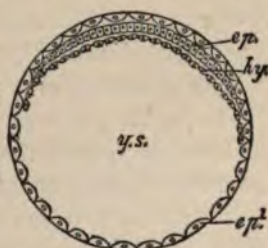
The outer-layer cells should be represented with large granules. The inner mass consists of finely granular protoplasm with imbedded nuclei, but it is impossible to distinguish the limits of the cells.



It would appear that this inner mass not only gives rise to a layer of flattened hypoblast cells by a differentiation of its inferior surface, but that it also gives rise principally, if not entirely, to the epiblast of the embryo. As will be immediately shown, the inner-layer disc corresponds with the early blastoderm of other Vertebrates, the greater portion of the outer-layer cells forming the external wall of the blastodermic vesicle; but they also extend

FIG. 41.—DIAGRAMMATIC SECTION OF A MAMMALIAN BLASTODERMIC VESICLE, IN WHICH THE PRIMITIVE INVAGINATION OF THE BLASTODERM IS RECTIFIED, AND THE COVERING CELLS HAVE EXTENDED OVER THE BLASTODERM.

ep. epiblast of future embryo; *ep'* non-embryonic epiblast, or the epiblast of the area opaca; *hy.* primitive hypoblast; *y.s.* yolk-sac.



as a covering layer (Deckenschicht) completely over the blastoderm proper. An extension of the hypoblast subsequently forms a second layer underlying the epiblast of the blastodermic vesicle.

The oosperm appears at this stage (fig. 41) as a vesicle, of which the upper half is three-layered, the layers being the covering layer, the epiblast, and the now differentiated hypoblast (fig. 41, *hy*), while the lower half consists for some time of a single layer of

epiblast. The covering cells, however, soon disappear, either entering into the formation of the embryonic epiblast or become attached to the decidua (see p. 92); in the latter case they would not form any portion of the embryo proper.

A translucent circular patch next appears at what corresponds with the upper pole of other oosperms (fig. 42), this embryonic area soon becomes ovoid and is homologous with the area pellucida of the Fowl. A primitive streak with its groove makes its appearance at the posterior end of the area. In the Mole, according to Heape, the blastoderm is perforated immediately in front of where the primitive streak is commencing to form (fig. 43, A); later this spot is marked by a small down-growth of the epiblast, which really corresponds with the anterior border of the blastopore. Somewhat more posteriorly a complete fusion takes place between the epiblast and incipient mesoblast (fig. 43, B), while at the pos-



FIG. 42.—RABBIT'S OOSPERM SEVEN DAYS AFTER IMPREGNATION. 3.47 mm. in length. Side view deprived of its envelope. Magnified about 10 diameters. [From Kölliker.]

ap. Area pellucida, or embryonic area; *pe.* inferior limit of the hypoblast; below this line the blastoderm consists solely of a single layer of epiblast.

terior end of the streak a complete fusion of all the layers occurs (fig. 43, C); but the three layers are distinct beyond the streak itself.

The similarity of a Mammalian blastoderm at this stage with that of a Bird, or especially of a Lizard, is very striking, and it led Balfour to propose the view that the Mammalian ovum originally possessed a large quantity of yolk, since the blastodermic vesicle is clearly homologous with the yolk-sac and contains a coagulable fluid comparable to some extent with the yolk. The primitive streak is the same structure in both Sauropsids and Mammals, that is, it represents a vanished blastopore.

It has since been proved by Haacke and Caldwell that the previously known but discredited fact was true that the Monotremata are oviparous, and that the eggs are in all essential points perfectly comparable with those of Reptiles. Thus Balfour's deduction from purely embryological data has been verified.

The primitive possession and the subsequent loss of food-yolk must be taken into consideration when dealing with the early stages of the development of the higher Mammalia. It has already been demonstrated how the presence of a large quantity of yolk is a

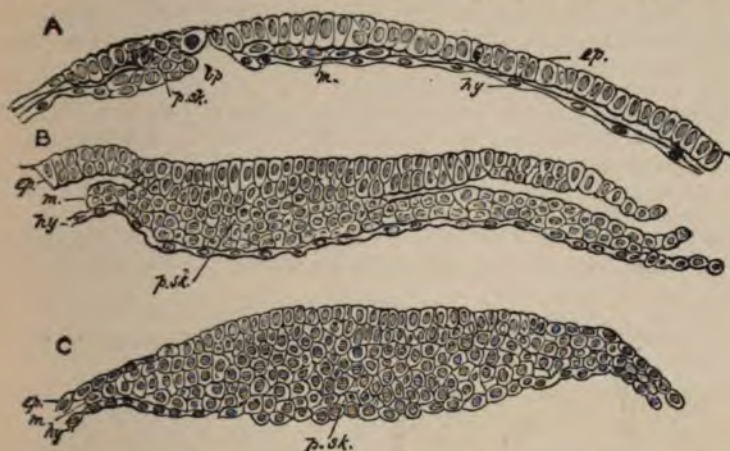


FIG. 43.—SECTIONS THROUGH THE BLASTODERM OF A MOLE (*Talpa*). [After Heape.]

A. Longitudinal section through the middle line of part of an embryonic area in which the primitive streak has commenced to form; the blastoderm is perforated in front of the primitive streak. B. Transverse section through the middle of a well-developed primitive streak; the epiblast and mesoblast are fused, but the hypoblast is distinct; the mesoblast here extends beyond the embryonic area. C. Same as B, but through the hind-knob of the primitive streak. All the layers are fused in the embryonic area, but are distinct beyond.

bp. blastopore; ep. epiblast; hy. hypoblast; m. mesoblast; p.sk. primitive streak.

disturbing factor; the subsequent loss of this would necessarily still further complicate matters.

Suggested Explanation of Mammalian Segmentation.—The following suggestions, previously published by the author, may perhaps tend to elucidate the apparent anomaly of the process of segmentation in a Mammalian oosperm. A somewhat similar hypothesis was independently arrived at by Minot.

FIG. 44.—DIAGRAMMATIC TRANSVERSE SECTION THROUGH THE BLASTODERM AND YOLK OF THE OOSPERM OF A HYPOTHETICAL PRIMITIVE MAMMAL.

ep. epiblast of future embryo; ep'. non-embryonic epiblast, which is surrounding the yolk; hy. primitive hypoblast; y. yolk.



The oosperm of a hypothetical primitive mammal (the Monotreme's oosperm is doubtless very similar to this) in which the yolk is still present is represented in fig. 44. The blastoderm, which rests upon the yolk, consists of an epiblastic layer and a mass of lower-layer cells; the yolk is being surrounded by the non-embryonic epiblast (ep').

An oosperm in which the yolk is supposed to have been lost is shown in fig. 45, A; and, owing to its absence, the yolk blastoderm or non-embryonic epiblast has precociously completed the blastodermic vesicle, and the blastoderm has sunk into the cavity of the now empty yolk-sac. This figure practically corresponds with the oosperm of the Bat figured above (fig. 40).

The inner mass is thus composed from the first of epiblast and primitive hypoblast, and the break in the outer layer ("blastopore" of Van Beneden) merely indicates the passage from the yolk blastoderm or area opaca to the embryonic blastoderm or area pellucida.

The increase of yolk during the evolution of a meroblastic from a primitively holoblastic oosperm results in a growth of the epiblast over the yolk. This also occurs in the Monotremata; but even after the yolk was lost this long-inherited tendency would persist; and since the yolk is absent, the completion of the overgrowth would necessarily be very precocious; so it comes about that in the Rabbit it is completed in about seventy hours (fig. 39).

In fig. 45, B, the epiblast has grown over the embryonic area, forming the covering cells (Deckenzellen). Lastly, the invagination of the embryonic area is rectified

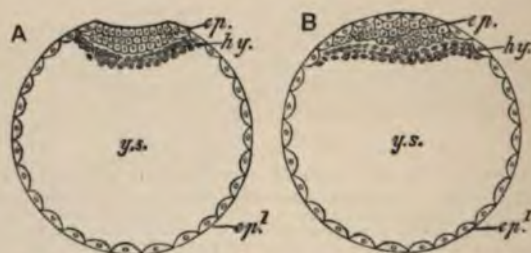


FIG. 45.—DIAGRAMMATIC TRANSVERSE SECTIONS THROUGH A HYPOTHETICAL MAMMAL OOSPERM.

A. Stage corresponding to figs. 40, a, and 41. The yolk of the primitive mammalian oosperm is now lost. B. Later stage, corresponding to fig. 39, c and d. The non-embryonic epiblast has grown over the embryonic area to form the covering cells.

ep. epiblast of embryo; ep'. epiblast of yolk-sac; hy. primitive hypoblast; y.s. yolk-sac or blastodermic vesicle.

(fig. 41), and there is a double-layered oosperm, the covering cells forming the spurious third layer, which misled Van Beneden into describing the oosperm at this stage as consisting of the three primitive germinal layers.

The completion of gastrulation, which in Vertebrates with meroblastic (telolecithal) oosperms is indicated by the appearance of the primitive streak, marks the close of the last stage of development which is common to all the Metazoa.

C. Gastrulation by Immigration and Delamination.—All the above-mentioned cases of gastrula formation may be reduced to one common type—invagination. There is, however, another series of phenomena which equally result in the formation of a double-layered from a single-layered embryo, which only occurs amongst the Hydromedusæ, and possibly in some Sponges.

The development of *Obelia* (fig. 46), which has been recently

studied by Merejkowsky, will serve as a type. The segmentation is regular, and results in a large oval blastula, the cells of which are equal in size and ciliated; the wall is also stated to be perforated by small pores. The embryo next becomes somewhat narrowed at the posterior end.* One by one the cells at the extreme hinder end of the embryo become amœboid and pass into the segmentation-cavity and wander about, congregating at first chiefly at the hinder extremity; eventually the entire segmentation-cavity is filled up by a cellular network formed by the fusion of the pseudopodia of these endoderm cells. Metschnikoff proposes the name "parenchymula" for such an embryo, which is formed of an ectodermal layer and a central solid mass of endodermal cells,

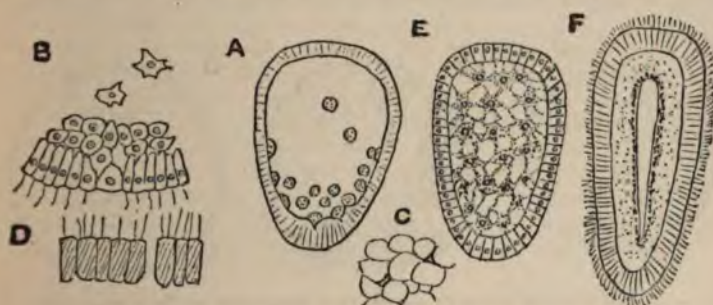


FIG. 46.—FORMATION OF THE PLANULA OF OBELIA. [After Merejkowsky.]

A. Longitudinal section of a blastula with a few scattered endoderm cells, chiefly at the hind-end. B. Posterior extremity of a slightly earlier stage, showing the proliferation of the terminal cell; the resulting endoderm cells immigrate into the segmentation-cavity. C. Surface view of a small area of a blastula with two pores. D. Section through a pore. E. Planula in which the segmentation-cavity is filled up with branched endoderm cells. F. Two-layered ciliated planula, with a definite archenteric cavity, but no mouth. After a short free life the planula becomes fixed.

but without a mouth. The term "planula" is usually applied to this and the succeeding stage. The endoderm now applies itself to the ectoderm as a definite layer, leaving a central cavity; the archenteron and the free-swimming planula is a ciliated elongated two-layered embryo, also destitute of a mouth. After a short free existence, the planula attaches itself by its anterior end, the ectoderm secretes a perisarc, a mouth and tentacles appear, and the hydroid stage commences.

In this type the endoderm is formed by immigration, which is positively stated to occur only at one pole of the blastula.

W. K. Brooks describes the planula of the Hydromedusoid

* The terms "anterior" and "posterior" have reference merely to the direction of progression of the larva.

Eutima as transparent and pear-shaped; he actually witnessed the inner ends of some of the ectoderm cells splitting off (delaminating) to form the endoderm; this takes place most rapidly at the small end, but endoderm cells are formed over the whole inner surface, and they arrange themselves in a single layer one cell thick around a central digestive cavity.

In the specialised Hydromedusa *Geryonia* (fig. 47), Fol describes the formation of the endoderm by delamination from all the primitive cells of the blastula; a mouth subsequently opens into the gastric cavity thus formed.

These three types appear to form a series, of which the first can scarcely be doubted to be the most primitive; and the formation of the endoderm by delamination may be regarded as derived secondarily from immigration.



FIG. 47.—SECTIONS THROUGH THREE STAGES IN THE SEGMENTATION OF GERYONIA. [After Fol.]

A. Stage of thirty-two cells; each cell is divided into an external, finely granular layer (indicated in the figure by shading) and an inner layer of clearer protoplasm. B. Later stage, in which the outer portion of the cells has given rise to a second cell, and the inner portions exhibit a protoplasmic reticulum. C. The endoderm (hypoblast) has been formed by a delamination of the inner portion of the cells; it now encloses the alimentary cavity (archenteron). The outer cells constitute the ectoderm.

In some Hydrozoa segmentation is stated to result in a solid mass of cells (Morula), the outer layer (ectoderm) of which is next split off from the internal solid mass. A central cavity appears in the latter; the cells bounding it are ultimately arranged as a single layer of endoderm.

Although there is still difference of opinion on the subject, the present evidence points to the view that immigration is closely allied to invagination, of which, indeed, it may be regarded a special form. Delamination has probably arisen through precociousness in the formation of the endoderm.

D. Segmentation and Gastrulation of Sponges.—There is so much diversity in the development of Sponges that it is at present impossible to reduce the variations to one common type, as can be done in other groups of animals.

Segmentation, which is fairly regular, results in the formation of a hollow blastula, the further development of which varies accordingly as a planula or an amphiblastula is formed.

The Planula.—The planula is a solid embryo consisting of an external columnar

flagellate ectoderm and a central gelatinous substance containing amoeboid cells. On becoming fixed the ectodermal cells are greatly flattened and lose their flagella, and a central cavity appears lined by a distinct endodermal epithelium, which in their turn become flagellate. The intermediate tissue persists as the mesoderm.

The walls of the central cavity bud off flagellate chambers into the mesoderm, and all the endoderm, excepting that which lines the chambers, is converted into a plate-like epithelium.

By perforations in its walls oscula and pores arise, and by various foldings of different parts the adult stage is reached. The structure of Sponges is, as a rule, greatly complicated by accelerated and retarded growth combined with conerescence and imperfect gemmation.

The Amphiblastula.—The amphiblastula is a hollow larva, one hemisphere being formed of granular amoeboid cells, the other of columnar flagellate cells. The latter (endoderm) eventually are invaginated within the former (ectoderm).

The hitherto free-swimming gastrula becomes attached by its blastopore. A middle layer (mesoderm) is now developed, apparently from the ectodermal cells [Metschnikoff], but this requires confirmation. The complications which succeed differ according to the group to which the embryo belongs.

Other methods of embryo-formation have been described, but the two above mentioned may be taken as fairly representative; the second appears to be almost confined to the Calcispongiae.

In all cases the spicules are of mesodermal origin. Nerve-cells and sense-cells have quite recently been described in a few forms by Stewart, Von Lendenfeld, and Sollas (p. 165), these are stated by Von Lendenfeld to be of mesodermal origin, as are also the unicellular glands and the muscle cells.

The Porifera form such a distinct and divergent group of the Metazoa that their development appears to have no direct bearing upon that of other Metazoa.

CHAPTER III.

FORMATION OF THE MESOBLAST.

As has been previously mentioned, a middle or third germinal layer early makes its appearance in ova between the epiblast and the hypoblast, which is known as the mesoblast or mesoderm.

Although the mesoblast is probably phylogenetically younger (that is, arose later in the evolution of the primitive Metazoa) than the gastrula stage, it not unfrequently, so to speak, is developed precociously; and throughout the animal kingdom the mesoblast may often be recognised very early in development. This is why it has been unavoidable to entirely omit any reference to the mesoblast when dealing with segmentation and gastrulation. In reading this chapter, it must be remembered that the formation of the mesoblast is synchronous with the phenomena previously dealt with.

There has been considerable difficulty in comprehending the nature of the mesoblast, owing to the fact of its diverse origin in the embryos of various animals; but, thanks to numerous recent researches, it is now possible to arrive at a more definite conclusion.

It is necessary to bear in mind that two entirely distinct structures are included under the single name of mesoblast or mesoderm; these have been termed "mesenchyme" [Hertwig] and "mesothelium" [Minot]. For the sake of clearness these will be considered apart.

1. Origin of the Mesenchyme.—In the embryos of a number of forms, amœboid cells are budded off during the blastula stage, either from the epiblast or the hypoblast, or from both layers. Minot has proposed the term "mesamœboids" for such wandering cells, instead of the more cumbersome titles of "mesenchyme germs" or "primitive mesenchyme cells" of Hertwig.

Mesenchyme alone is present in Sponges; the mesoderm consisting in this group of mesamœboids derived in the adult from the

endoderm cells, although it is stated to arise from the ectoderm in the embryo.

In the Coelenterata the mesoderm may be represented only by the structureless lamella, as in *Hydra*; or by gelatinous tissue in which are scattered stellate cells (mesamœboids) mostly of hypoblastic origin in the Scyphomedusæ, and mainly of epiblastic origin in the Ctenophora.

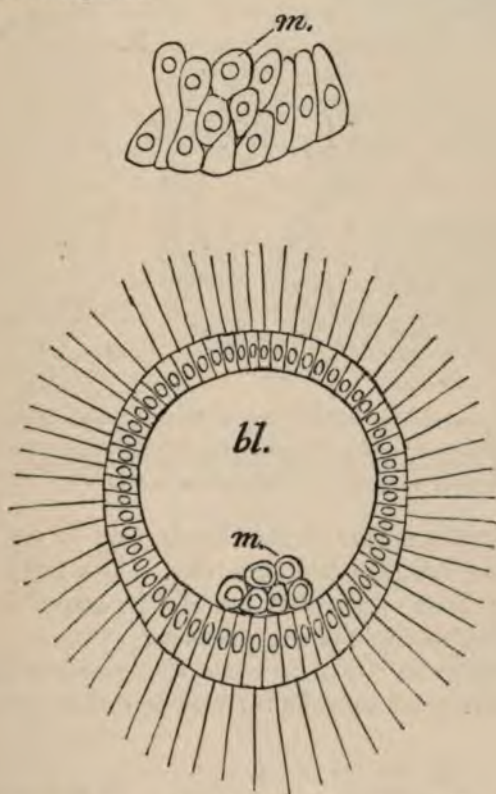


FIG. 48.—BLASTULA OF ECHINUS; drawn from the living embryo. [After Metschnikoff.]

A. Mesamœboids arising from the hypoblastic pole of the blastula. B. Later stage; the blastula is ciliated.
bl. blastocœl; m. mesamœboids.

During, or even anterior to, the invagination of the archenteron in Echinoderms (fig. 16), mesamœboids are budded off from the incipient hypoblast (fig. 48). These cells wander throughout the segmentation-cavity and adhere to all the organs as they are formed, thus forming a mesoblastic investment.

In the Platyhelminth *Lineus obscurus*, Hubrecht has recently shown that the mesamœboids arise during the gastrula stage from

the epiblast and hypoblast (fig. 49), but mainly from the latter; and it is probable that the truly mesoblastic organs are derived solely from the latter (see p. 165). In *Leptoplana*, four primitive mesoblast cells are segmented from the four yolk-hypoblast cells, and very soon they come to be situated at the lips of the blastopore. As the epiblast grows over the yolk-hypoblast (fig. 50), the meso-

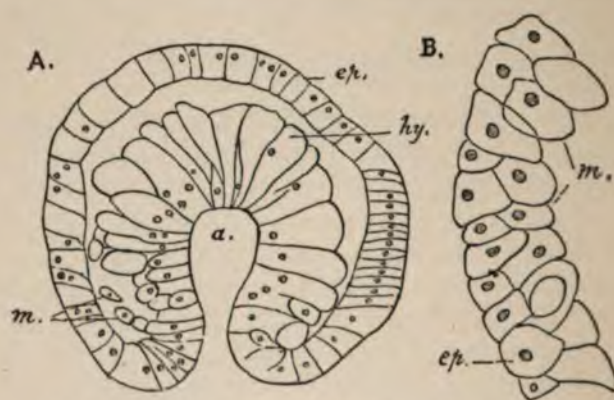


FIG. 49.—ORIGIN OF MESENCHYME IN *LINEUS*. [After Hubrecht.]

A. Gastrula stage; mesomæboids are seen arising from the hypoblast. B. Later stage, in which the epiblast is giving origin to mesomæboids. a. archenteron; ep. epiblast; hy. hypoblast; m. mesoderm.

blasts, which now appear as four bands, pass to the upper pole and obliterate the segmentation-cavity. The large amount of yolk present in the hypoblast has clearly exerted a disturbing influence upon the origin of the mesoblast.

In the *Discophora* the mesoblast early forms two bands, which arise from cells which must be regarded as yolk-hypoblast.

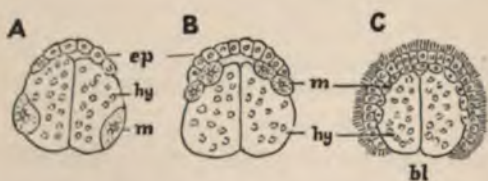


FIG. 50.—GASTRULATION AND ORIGIN OF MESOBLAST IN *LEPTOPLANA TREMELLARIS*. [After Hallez.]

bl. blastopore; ep. epiblast, ciliated in C; hy. yolk cells (primitive hypoblast); m. mesoblast.

Stellate mesoblast cells, which may be considered as mesenchymatous, traverse the space between the epiblast and archenteron in the free-swimming larvæ of some Polychæte Worms (*Serpula*) before the true cœlom is developed. Similar cells are also to be found in the pre-oral lobe of embryo Oligochætes.

In the Mollusca, as a whole, the mesoblast is derived from cells intermediate in position between the epiblast and the hypoblast (fig. 18), but which may be considered as belonging to the latter rather than to the former.

The presence of mesenchyme in any of the higher Metazoa must for the present be regarded as an open question.

2. Origin of the Mesothelium.—Paired outgrowths from the archenteron, which ultimately become constricted off as closed sacs, make their appearance on the completion of the gastrula stage in such diverse groups of the Metazoa as the following:—All the Echinodermata; the Chætogonatha (*Sagitta*); Brachiopoda (fig. 51); *Peripatus* (fig. 69); *Balanoglossus*; and *Amphioxus*

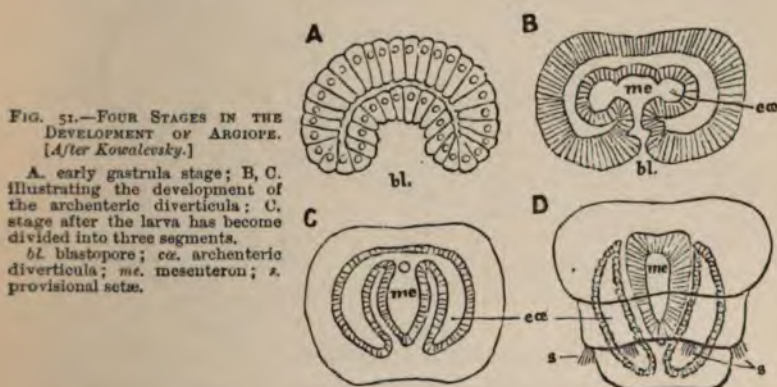


FIG. 51.—FOUR STAGES IN THE DEVELOPMENT OF ARGIOPE. [After Kowalevsky.]

A. early gastrula stage; B, C. illustrating the development of the archenteric diverticula; C. stage after the larva has become divided into three segments. bl. blastopore; ca. archenteric diverticula; me. mesenteron; s. provisional setæ.

(fig. 56). The cavity of these sacs will form the body-cavity or coelom of the adult, and the walls constitute such mesothelial tissues as the peritoneum, mesentery, muscles, and the excretory and generative organs.

Amongst the Echinodermata a pair of such diverticula usually arise from the blind end of the archenteron; sometimes only a single vesicle is constricted off, which immediately divides into two. The former is probably the more primitive mode. These two sacs enlarge and lie one on each side of the archenteron (fig. 52); the left further gives rise to the third vesicle, which by radial prolongations develops into the ambulacral system of these animals. The two remaining sacs eventually increase in size, so as to fill up the whole of the segmentation-cavity. The alimentary canal thus comes to be surrounded by the two vesicles: when these meet each other in the middle line, their applied walls

become more or less absorbed, the remains forming the mesentery of the adult, and the conjoint cavities constitute the coelom or body-cavity proper. It will be remembered that there exists a layer of mesenchyme between the epithelium of the body-cavity (mesothelium) on the one hand, and the epiblast of the body-wall and the hypoblast of the alimentary canal on the other.

With the exception of not giving rise to an ambulacral system, and a possible absence of mesenchyme in some, the formation of the coelom is practically identical in the above-mentioned forms with that of the Echinoderms.

Conn has recently stated that in *Serpula*, which appears to have

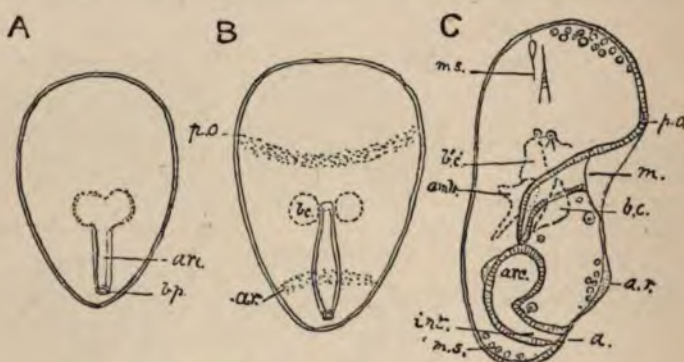


FIG. 52.—THREE LARVAL STAGES OF THE STAR-FISH (*Asterias*).

A. Late gastrula stage, with commencing archenteric diverticula. B. Coelomic pouches constricted off. C. Early larval stage, with stomodæum not yet opening into the mesenteron; the left coelom has formed the rudiment of the ambulacral system.

a. anus (persistent blastopore, bp.); amb. primitive ambulacral vesicle; a.r. anal ring of cilia; arc. archenteron (mesenteron in C.); b.c. right, and b.c. left coelomic sac; int. intestine; m. mouth (stomodæum); ms. mesamœboids; p.o. pre-oral ciliated band.

a more simple development than most other Chætopods, the mesoblast arises at the posterior end of the elongated blastopore. At first stellate mesenchyme cells are formed which stretch across the segmentation-cavity, and some of which enclose a small posterior vesicle (anal vesicle). The remaining mesoblast cells rapidly give rise to two bands of cells, one on either side of the alimentary canal, and extending forwards to the mouth: these "mesodermal bands" segment and become hollow, thus forming the many-chambered body-cavity, and giving rise to the usual mesoblastic structures. In one Earthworm (*Lumbricus trapezoides*) the mesoblast is partly derived from "mesoblasts" which are distinguishable before the segmentation-spheres are arranged

into distinct layers; but Kleinenberg inclines to the view that they are epiblastic in origin. The mesoblasts by cell-division form a pair of latero-ventral mesoblastic bands, which further develop as in *Serpula*. As the development of the *Oligochæta* is undoubtedly abbreviated, the origin of the mesoblast is consequently liable to be modified.

In the Fresh-water *Oligochæte Rhynchelmis* (Euaxes), as a considerable amount of yolk is present, the gastrulation is epibolic. The chief portion of the mesoderm arises very early from two mesoblasts, which are derived from the primitive hypoblast cells. The two mesoblastic bands occur at the junction of the epiblast with the hypoblast (fig. 53).

There is considerable uniformity in the accounts of the origin of the mesoblast amongst the Crustacea. It may be formed by paired

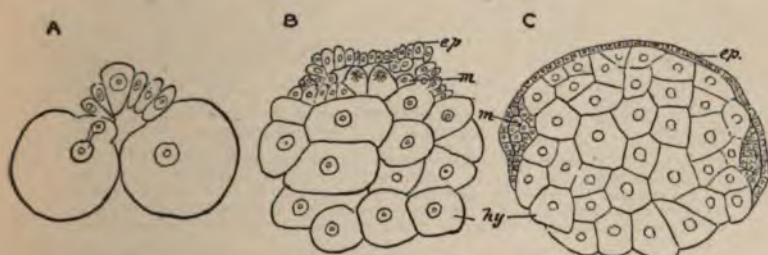


FIG. 53.—GASTRULATION AND FORMATION OF MESOBLAST IN *RHYNCHELMIS* (EUAXES).
[After Kowalevsky.]

A. Section through blastula stage of twenty cells. B. Late blastula stage, with commencing mesoblast. C. Epibolic gastrula with paired mesoblastic bands.
ep. epiblast; hy. yolk, or primitive hypoblast; m. mesoblast.

proliferations from the hypoblast cells of the neck of the archenteron during gastrulation (fig. 54), or from one or a pair of cells which, in the blastula stage, occupy a position between the future epiblast and hypoblast, and which sink into the segmentation-cavity. It is probable that the latter case is merely a precocious abbreviation of the former. The presence of mesenchyme in this group is not yet satisfactorily established, though Reichenbach has described the development of what he terms "secondary mesoblast" from the hypoblast cells of the Crayfish (fig. 54, F) on the completion of the gastrula stage.

The origin of the mesoblast in the Tracheate Arthropoda is still obscure. In Insects it is partly derived from a ventral groove of the epiblast, and in Spiders from an analogous solid keel. The latter is probably a modification of the former process, and Balfour

has homologised the mesoblastic groove of Insects with the blastopore of a vanished gastrula stage. In both groups the mesoblast

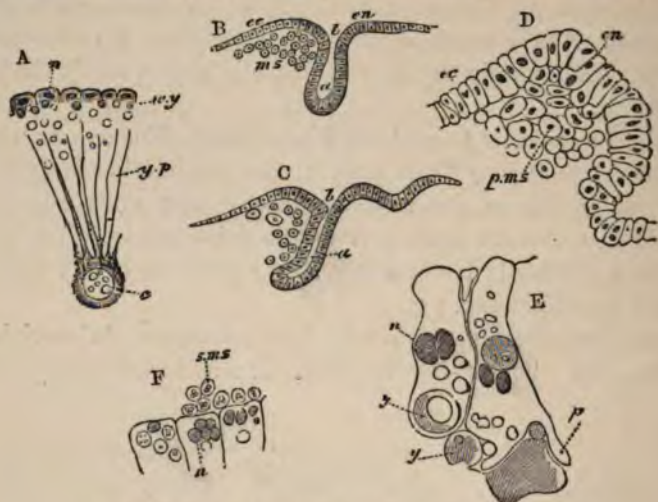


FIG. 54.—FIGURES ILLUSTRATING THE DEVELOPMENT OF *ASTACUS*.
[From T. J. Parker after Reichenbach.]

A. Section through part of oosperm during segmentation. B and C. Longitudinal sections during the gastrula stage. D. Highly magnified view of the anterior lip of blastopore, to show the origin of the primary mesoblast from the wall of the archenteron. E. Two hypoblast-cells to show the intra-cellular digestion of yolk-spheres. F. Hypoblast-cells giving rise endogenously to the secondary mesoblast.

a. archenteron; b. blastopore; c. central yolk mass; ec. epiblast; en. hypoblast; n. nuclei; p. pseudopodial process; p.ms. primary mesoblast; s.ms. secondary mesoblast; w.y. white yolk; y. yolk spheres; y.p. yolk pyramids.

appears to be added to by cells arising from the yolk-hypoblast. A pair of mesoblastic bands soon appear, much as in the Chæto-



FIG. 55.—DIAGRAMMATIC REPRESENTATION OF AN IDEAL GASTRULA STAGE OF AN INSECT AT THE TIME WHEN THE ARCHENTERIC DIVERTICULA ARE FORMED. [After O. and R. Hertwig.]

bl. blastopore; ep. epiblast; hy. mesenteric hypoblast; m. parietal or somatic layer of mesoblast—between this and the hypoblast is the visceral or splanchnic layer of mesoblast; n. nerve cord; y. yolk-cells or primitive hypoblast.

Pods, which similarly segment, each segment containing a portion of the coelom.

In all the invertebrate groups the mesoblast mainly arises from cells which grow inwardly from the lip of the blastopore. In closely allied forms the primitive cells

vary from an apparently epiblastic to an apparently hypoblastic, or to an intermediate place of origin. The extreme variations may be neglected, as being in all probability of only secondary significance.

Since this was in type Sedgwick has shown that the somites in *Peripatus* (fig. 69) do not directly arise as archenteric diverticula, but are separated from a pair of mesoblastic bands as in *Chaetopoda*. The somites are at first ventro-lateral in position, but soon acquire a dorsal extension and divide into two parts. The dorsal parts come into contact above the enteron, but do not unite with their fellows; anteriorly they are early obliterated, but persist posteriorly as the generative glands. The ventral moieties remain distinct, and consist of a small vesicle situated in the base of the appendages, leading from which is a small coiled tube (nephridium), which acquires an external opening. The Hertwigs have interpreted the formation of the mesoblast in Insects in terms of archenteric diverticula (fig. 55), but the undoubtedly primitive character of *Peripatus* renders its development especially important. Although the cavities of mesoblastic bands and archenteric diverticula are homologous, their exact relation to one another is somewhat obscure.

Whatever views may be held as to the precise position of the *Chaetognatha*, *Brachiopoda*, and *Balanoglossus*, the presence of archenteric diverticula in these

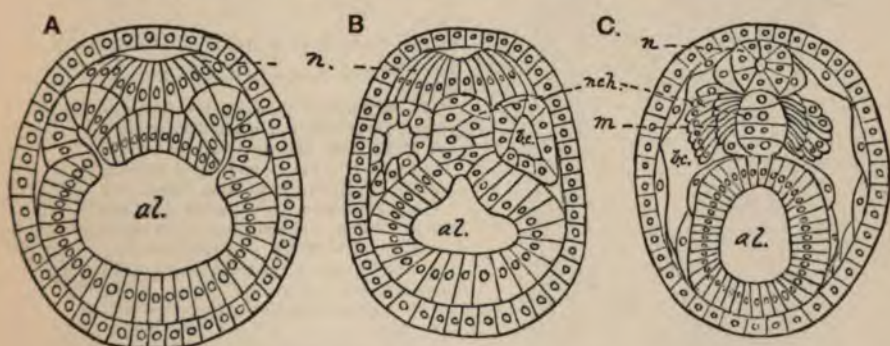


FIG. 56.—TRANSVERSE SECTIONS OF EMBRYOS OF AMPHIOXUS. [After Hatschek.]

A. Section through the first somite or primitive segment of an embryo in which the fifth somite is being formed. B. Section through the same region of an embryo with eight somites. C. Section through the centre of the body of an embryo with eleven somites.

al. mesenteron; bc. coelom; m. muscle fibres; n. neural plate and canal; nch. notochord.

forms proves that it occurred in several of the primitive Worms; so it may be safely concluded that the mesoblast (for the most part, at all events) of the Gephyrea, Polyzoa, and Nematoda belongs to this category.

It will probably be shown that mesothelial mesoblast occurs also in all Mollusca. It is probable that the pericardium of this group represents the true body-cavity of other orders; but even if this is the case, there would be a marked preponderance of mesenchyme over mesothelium in the mesoblast.

There are not sufficient data to come to a definite conclusion concerning the exact nature of the mesoblast of the Platyhelminths.

Origin of the Mesoblast in the Chordata.—There appears to be no valid reason for refusing to accept Bateson's conclusion that *Balanoglossus* is a persistent representative of an early stage

in the evolution of the Chordata from the unsegmented Worms. He has extended the observation of others that the mesoblast in this remarkable form is derived from archenteric diverticula in a manner very similar to that which is characteristic of the Echinodermata. But the details of mesoderm formation in this form and in the Tunicata must be passed by.

In *Amphioxus* the formation of the mesoblast is of remarkable simplicity. The development of this form (p. 29) was traced to

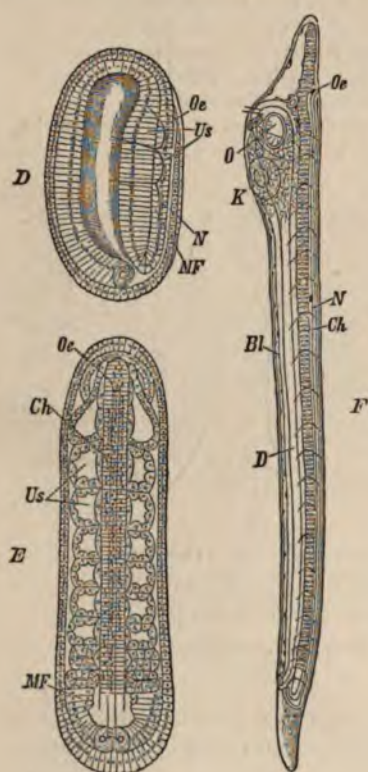


FIG. 57.—THREE LARVAL STAGES OF AMPHIOXUS.

[From Claus, after Hatschek.]

D. Stage with two somites (primitive segments), seen in optical longitudinal section. E. Stage with nine somites, seen from above, showing the asymmetry of the segments. F. Living larva with mouth and first gill-slit, seen from the left side; the second, fourth, and sixth bent lines represent respectively the posterior boundary of the first, second, and third somite of the opposite (right) side.

Bl. ventral blood-vessel; Ch. notochord; D. intestine; K. gill-slit; MF. unsegmented mesoderm fold; N. neural canal; O. mouth; Oe. anterior orifices of neural canal; Us. somites.

an elongated gastrula stage with a dorso-posterior blastopore. Two small pouches soon arise from the archenteron (fig. 56, A) near the anterior end of the embryo, one on each side of the median dorsal line. These are followed by others, which are successively developed from before backwards (fig. 57, D, E). These extend laterally along the dorsal side of the embryo; but, as seen in fig. 57, E and F, they are not placed symmetrically opposite one another.

The archenteric diverticula very shortly become constricted off from the archenteron, or mesenteron, as it should now be termed (fig. 56, B), and form a series of closed sacs (mesoblastic somites or primitive segments). Each somite encloses a distinct cavity or coelom. The somites gradually extend in a ventral direction, enclosing the alimentary canal (mesenteron) (fig. 56, C); and by the subsequent fusion of their cavities form the small coelom or body-cavity of the adult.

The outer layer of the somites is known as the somatic or peripheral mesoblast, the inner layer being termed the splanchnic or visceral mesoblast. The dorsal moities of the somites lose their cavities, and become transformed into the great lateral muscle of the larva and adult; but the primitive segmentation is permanently retained.

It is readily apparent (fig. 56, A) that the mesoblast is derived from two regions of the hypoblast. The ventral layer is continuous with the digestive portion of the hypoblast; while the dorsal half is derived from the axial hypoblast. The remainder of this latter is converted into the notochord (fig. 56, B, *nch*). The separation of the somites and the notochord from the archenteron appears to be due to the dorsal growth and coalescence of the digestive hypoblast below these structures. The cavity of the archenteron equals that of the mesenteron + the coeloms of the mesoblastic somites.

There would seem to be no mesenchymatous elements in the mesoblast of *Amphioxus*, unless the pair of "hinder-pole mesoderm cells" (fig. 23) are to be regarded as such. They arise from the hypoblast at the ventral lip of the completed gastrula, and are stated by Hatschek to give rise solely to the caudal mesoderm.

The origin of the mesoblast in the Newt (*Triton*) is very instructive, as it serves to elucidate the formation of the mesoblast in *Reptilia* and to reduce the latter to the type of *Amphioxus*. On the completion of the gastrula stage the mesoblast is only to be found close to the blastopore (fig. 58). The main portion grows out as a pair of lateral sheets dorsal to and at each of the blastopore (fig. 58, B, *m*). The brothers Hertwig at first described the mesoblast as composed from the commencement of two distinct layers, the outer growing from the epiblast of the lips of the blastopore, and the inner from the primitive hypoblast. Each lateral sheet is, however, at first a solid mass of cells, which gradually extends forwards and downwards, *i.e.*, anteriorly and ventrally. According to Scott and Osborn, the lateral meso-

blast also increases at the expense of the yolk-hypoblast. The mesoblastic sheets very early split into two layers, an external somatic and an internal splanchnic. The cavity between the two layers extends ventralwards, and forms the body-cavity or coelom. The anterior extension of the paired or dorsal mesoblast appears

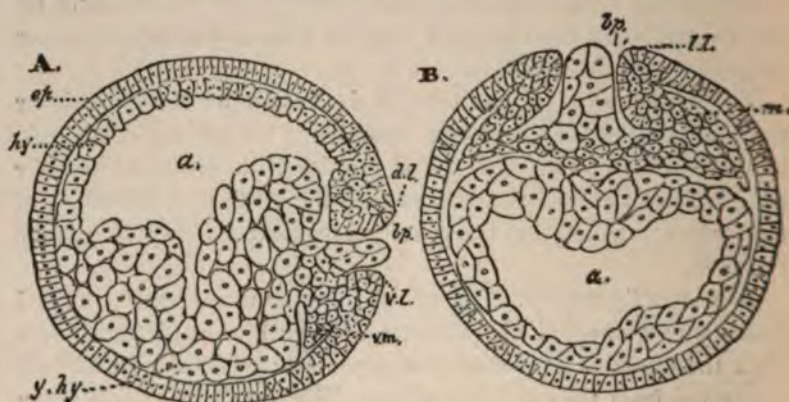


FIG. 58.—LATE GASTRULA STAGE OF THE NEWT (TRITON). [After O. Hertwig.]

A. Median vertical longitudinal section. B. Horizontal section through the same.

a, archenteron; bp, blastopore; d.l, dorsal lip of blastopore; ep, epiblast; hy, dorsal or axial hypoblast; l.l, lateral lip of blastopore; m, dorsal mesoblast; v.l, ventral lip of blastopore; v.m, unpaired ventral mesoblast; y.hy, yolk-hypoblast.

to occur at the expense of the hypoblast, in a similar manner to that described for *Amphioxus* (fig. 59). Hertwig describes the dorsal layer as arising from the "Chorda-entoblast" (axial or notochordal hypoblast), and the ventral from the "Darm-entoblast" (digestive or gut hypoblast).



FIG. 59.—TRANSVERSE SECTION OF THE DORSAL PORTION OF AN EMBRYO NEWT (TRITON). [After O. Hertwig.]

a, mesenteron; ax.hy, axial hypoblast in process of forming the notochord; b.c, coelom (body-cavity); ep, epiblast; hy, digestive hypoblast; np, neural plate; som, somatic mesoblast; sp.m, splanchnic mesoblast.

In the Newt, and all the higher Chordata, as in *Amphioxus*, the axial hypoblast or notochord is in direct contact with the neural epiblast, consequently the dorsal mesoblast is distinctly paired. There is a ventral growth of unpaired mesoblast from the lower lip of the blastopore (fig. 58, A, v, m). This occurs at the

spot where the epiblast and hypoblast pass into each other, and it is difficult to say which layer has the larger share in its formation; if either, it is perhaps the epiblast.

The formation of the mesoblast in the Lamprey is, according to Calberla, practically identical with that in the Newt; in some

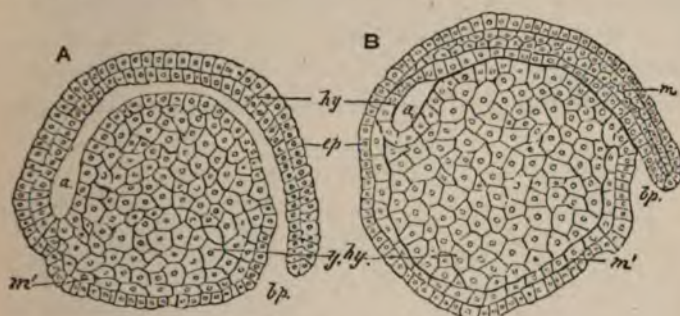


FIG. 60.—LATE GASTRULA STAGE OF LAMPREY. [After Scott.]

A. Median longitudinal vertical section. B. Section to one side of A. The relation of the hypoblast to the mesoblast is more clearly seen in fig. 61. a, archenteron (mesenteron); bp, blastopore; ep, epiblast; hy, hypoblast of mesenteron, axial hypoblast in A; m, paired mesoblast; m' ventral unpaired mesoblast; y.hy, yolk-hypoblast.

respects it is simpler than in the latter, owing to less food-yolk being present in the ovum. The position of the paired mesoblast is clearly shown in figs. 60 and 61. The two latero-dorsal sheets extend from the lip of the blastopore some distance forwards, but

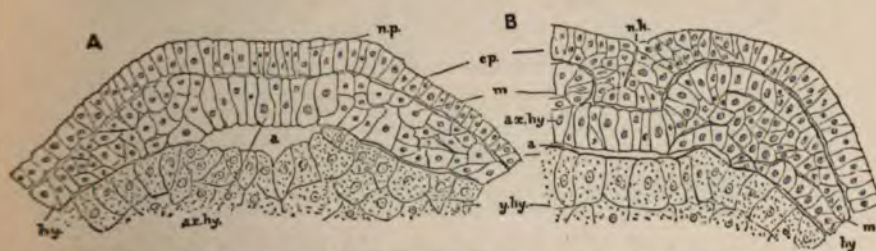


FIG. 61.—TRANSVERSE SECTIONS THROUGH THE UPPER PORTIONS OF TWO EMBRYO LAMPREYS (*Petromyzon plaueri*). [After Calberla.]

A. Some stage as fig. 63. B. Later stage. a, archenteron; ax.hy, axial (notochordal) hypoblast; ep, epiblast; hy, (digestive) hypoblast; m, mesoblast; n.k, neural keel; n.p, neural plate; y.hy, yolk-hypoblast.

they have not yet acquired any lateral or rather ventral extension; dorsally they are separated from one another by the axial hypoblast (figs. 60, A, and 61, A).

According to Scott, a single layer of mesoblast (fig. 60, m) surrounds the lateral and ventral surface of the yolk-hypoblast

from which it is derived; he also states that the paired mesoblast grows forward from the blastopore, and that it does not exhibit any intimate relation with the axial hypoblast.

In his recently published paper, Shipley states that in *Petromyzon fluviatilis* the first formation of the mesoblastic plates appears to take place by a differentiation of the hypoblastic yolk-cells *in situ*, and not from invaginated cells. The subsequent downward growth is brought about by the cells proliferating along the free ventral edge of the mesoblast; these cells then growing

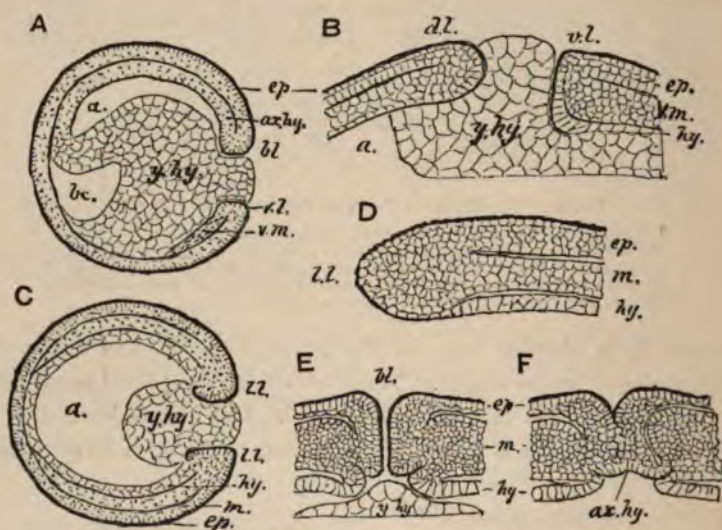


FIG. 62.—ORIGIN OF MESOBLAST IN THE FROG. [After O. Hertwig.]

A. Median longitudinal vertical (sagittal) section through a gastrula with a wide blastopore. B. Enlarged view of a portion of the same. C. Horizontal (frontal) section through a stage similar to that of A. D. Lateral lip of a corresponding stage. E. Horizontal section through a nearly closed blastopore. F. Section through the anterior lip of a closed blastopore.
a. archenteron; ax.hy. axial hypoblast; bc. blastocoeil; bl. blastopore; d.l. dorsal; l.l. lateral; v.l. ventral lip of blastopore; ep. epiblast; hy. hypoblast; m. lateral mesoblast; v.m. ventral mesoblast; y.hy. yolk hypoblast.

ventralwards push their way between the yolk-cells and the epiblast.

In the Frog the mesoblast has a fundamentally similar origin to that above described, but the invagination of the mesoblast is less marked. The greater portion of the mesoblast is apparently derived by the metamorphosis of the small cells of the yolk-hypoblast *in situ* (figs. 24 and 62); the result being that there is very early a sheath of mesoblast, one or more cells thick, below the epiblast. The mesoblast is only interrupted along the median dorsal line. The explanation of figs. 24 and 62 sufficiently illus-

trate the character of the mesoblast of the Frog on its first appearance.

Mitsukuri and Ishikawa have very recently shown that in the Turtle (*Trionyx*) the formation of the mesoblast closely recalls the same process in the Newt. Fig. 63, which represents a transverse section through the hind-portion of the head, demonstrates the paired mesoblast as arising by proliferation from the hypoblast at the spot where the digestive hypoblast is contiguous with the

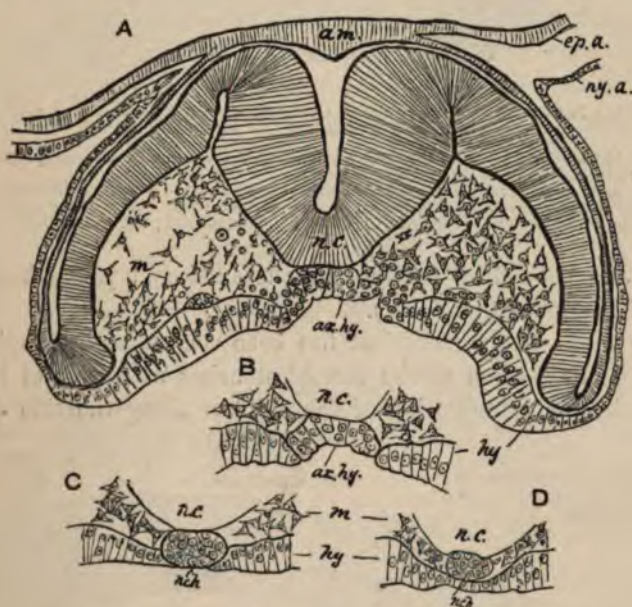


FIG. 63.—MESOBLAST OF TRIONYX. [After Mitsukuri and Ishikawa.]

A. Transverse section through the head region before the closure of the neural groove. B-D. Portions of successive sections of the same embryo.
am, amnion; ax.hy, axial hypoblast; ep.a, epiblastic layer of amnion; ny.a, hypoblastic layer of amnion; hy, hypoblast; m, mesoblast; n.c, neural canal; nch, notochord.

axial or notochordal hypoblast. In this case, as in so many other instances, the proliferation may be regarded as a degenerate form of invagination.

Behind the blastopore the mesoblast arises, as in Amphibia, as an unpaired mass, and in this region there is a fusion of the three germinal layers, thus forming a primitive streak.

The formation of the mesoblast in the Lizard (fig. 64) is intermediate between that which occurs in the Turtle and the Fowl. The paired mesoblast has much the same origin as that to be

shortly described for the Fowl. It arises posteriorly from the walls of the blastopore as a pair of lateral sheets, which are free for the greater portion of their extent, but are fused in the median line of the posterior region of the embryo with the axial hypoblast. Anteriorly the mesoblast is derived from branched cells,



FIG. 64.—TRANSVERSE SECTION THROUGH A PORTION OF THE BLASTODERM OF A LIZARD (*Lacerta muralis*). [After Weldon.]

The section illustrates the double origin of the mesoblast in the embryonic region, i.e., in front of the primitive streak.

a. mesenteron; ax.hy. axial hypoblast, which is about to develop into the notochord; ep. epiblast; hy. hypoblast; m. mesoblast, partly derived from the axial, and partly from the permanent hypoblast; n.f. neural fold; n.g. neural groove.

which are budded off partly from the axial, and partly from the lateral hypoblast (fig. 64, m).

The origin of the mesoblast has been very carefully studied in Birds. One portion of the mesoblast arises as a pair of lateral plates by the proliferation of the epiblast along the line of the

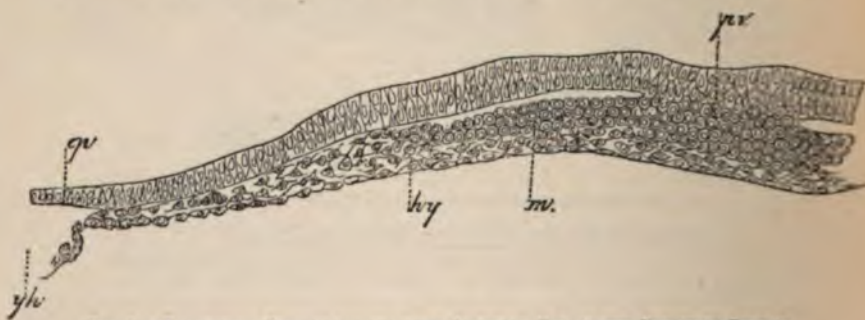


FIG. 65.—TRANSVERSE SECTION THROUGH THE ANTERIOR END OF THE PRIMITIVE STREAK OF A FOWL'S BLASTODERM ABOUT THE AGE OF FIG. 34. [From Balfour.]

Showing the rounded mesoblast cells arising from the primitive streak and the stellate cells of hypoblastic origin.

ep. epiblast; hy. hypoblast; m. mesoblast; p.v. primitive groove; y.g. yolk of germinal wall.

primitive streak (fig. 65). Balfour even says that during this period many sections through the primitive streak give an impression of the mesoblast being involuted along the lips of a groove. A second portion of the mesoblast is that which gives rise to the lateral plates of mesoblast in the head and trunk of the

embryo. This is formed of stellate cells, which are at first readily distinguishable from the rounded cells of the former class; they arise from the hypoblast mainly on each side of the median line, and especially in the region in front of the primitive streak; in other words, in the embryonic region. They are continuous behind with the lateral wings of mesoblast which grow out from the primitive streak, and on their inner side are also at first continuous with the cells which form the notochord.

The third portion of the mesoblast is derived partly from those cells of the lower-layer cells which do not form the permanent hypoblast, and which are scattered between that layer and the epiblast (figs. 30-34), and partly from the germinal wall, or that ridge of cells, nuclei, and yolk-granules which in the early stages



FIG. 66.—SECTION THROUGH THE GERMINAL RIDGE OF A FOWL'S BLASTODERM. [After Kollmann.]

a. archenteron; *ep.* epiblast; *hy.* hypoblast; *m.* mesoblast cells (mesamoeboids or "Poreuten") which have been derived from the primitive hypoblast cells of the germinal ridge; *y.* yolk; *y.* yolk-spheres ingested by the primitive hypoblast.

of incubation forms the marginal boundary of the lower-layer cells or primitive hypoblast (figs. 65, 66). The large primitive hypoblast cells of the germinal wall are undoubtedly nutritive in function, and ingest the underlying yolk. By cell-division they give origin to amœboid wandering cells (fig. 66, *m.*), which are stated by Kollmann to form the primitive vascular system, the blood, and also the connective tissue. In either case, the cells have the same morphological value since they are derived from lower-layer cells before the hypoblast proper is differentiated.

While the paired mesoblast referred to above is clearly mesothelial in character, the mesoblast which arises from the lower-layer cells and the germinal wall appears to be mesenchymatous in nature.

The development of the mesoblast in the Mole (*Talpa*) (fig. 67) has been shown by Heape to agree very closely with that de-

scribed above for Birds. Posteriorly the mesoblast arises where the epiblast and hypoblast are fused at the primitive streak, and clearly owes its existence to both. In the region in front of the primitive streak the mesoblast is proliferated from the hypoblast as two lateral masses which posteriorly unite with the above-mentioned mesoblast. There also appears to be an actual continuity between the developing notochord and the dorsal portion of the paired mesoblast.

There is some diversity of opinion amongst other investigators concerning the origin of the mesoblast amongst Mammals. It may be concluded that the Mole, being an Insectivore, would probably not have a very specialised development for

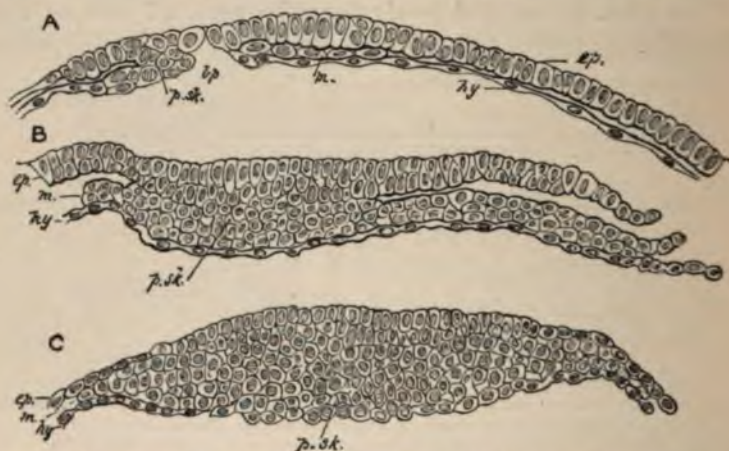


FIG. 67.—SECTIONS THROUGH THE BLASTODERM OF A MOLE (*Talpa*). [After Haepe.]

A. Longitudinal section through the middle line of part of an embryonic area in which the primitive streak has commenced to form; the blastoderm is perforated in front of the primitive streak. B. Transverse section through the middle of a well-developed primitive streak; the epiblast and mesoblast are fused, but the hypoblast is distinct; the mesoblast here extends beyond the embryonic area. C. Same as B. but through the hind-knob of the primitive streak. All the layers are fused in the embryonic area, but are distinct beyond, *bp.* blastopore; *ep.* epiblast; *hy.* hypoblast; *m.* mesoblast; *p.sk.* primitive streak.

a Mammal, and, for the present, the above statement may be regarded as holding good for Mammalia generally.

When the embryology of the Prototheria (*Ornithodelphia*) is investigated, it will doubtless be found to resemble that of the Lizard in many points, and will demonstrate that any peculiarities in the development of Mammals is due first to the presence, and secondly to the subsequent loss, of food-yolk.

Although in most Vertebrates the mesothelial mesoblast is at first solid, it very shortly splits into two layers, a peripheral or somatopleur, and a visceral or splanchnopleur (figs. 59, 71). The pleuro-peritoneal cavity or coelom thus produced is strictly homologous with the persistent body-cavity of such forms as have hollow archenteric diverticula.

It is evident from the foregoing summary that the derivation of the true body-cavity or coelom from archenteric diverticula occurs in one or more examples of

nearly all the main groups of the animal kingdom. In the majority of cases it occurs in generalised, or, geologically speaking, in ancient types. It may then be safely concluded that this is the primitive method of the formation of the coelom. This statement does not preclude the possibility of interstitial spaces or cavities occurring, as in Platyhelminthes, Arthropoda and Mollusca; but these, not being lined by an epithelium derived from the archenteron, should always be distinguished as pseudocoelous or archicoelous cavities, as opposed to a true body-cavity. It is known that mesodermal (mesenchymatous) cells bounding a pseudocoel (archicoel), or cavities derived therefrom, may sometimes become flattened and form an endothelium.

There can be no doubt that the lateral sheets of mesoblast of Vertebrates with telolecithal ova are identical with the mesoblastic somites of *Amphioxus*, and the latter again with the archenteric diverticula of many Invertebrates.

A very instructive series can be traced from such an alecithal ovum as that of *Amphioxus* through the Lamprey, Newt, Frog, Turtle, and Lizard, to the extreme telolecithal type of the Bird. The lateral proliferation of the hypoblast in the Lizard and Fowl (figs. 64, 65) to form the mesoblast is possibly a secondary process. Throughout this series the axial hypoblast takes its share in formation of the paired mesoblast along with what has been spoken of as the digestive hypoblast.

The primitive-streak mesoblast, as it is termed, is the equivalent of the mesoblast which arises from the lips of the blastopore; as, for example, in the Newt. A reference to the section dealing with telolecithal gastrulation and the nature of the primitive streak will render further comment needless.

Allusion has previously been made to the origin of certain indifferent mesoblast cells from the primitive hypoblast, which appear to differ in character from the former, and which have been regarded as being mesenchymatous in nature.

Summary.—The following is a brief *resumé* of the mesoblastic elements of the Metazoa.

Mesamœboids arise, apparently indiscriminately, from the endoderm (hypoblast) of larval and adult Sponges, and from the same layer in Coelenterates. The cells which migrate from the ectoderm into the gelatinous tissue in the latter group are practically epiblastic mesoderm. In most of the Coelenterates archenteric diverticula are found, which never become separated from the alimentary canal.

In the Echinoderms, mesamœboids arise in the blastula stage, chiefly, if not entirely, from the incipient hypoblast; and after the formation of the gastrula, archenteric diverticula arise, which become completely shut off to form the body-cavity of the adult.

The mesamœboids of the Platyhelminths are derived, in some cases, at all events, from both layers of the gastrula.

The exact nature of the mesoblast of Molluscs has not yet been satisfactorily demonstrated.

The Arthropods and their ancestors, the Segmented Worms, possess an enterocoelous body-cavity, although, in the great majority of cases, its method of development masks its real nature. The presence of mesenchymatous mesoblast in these groups has been questioned.

Lastly, in Vertebrates the mesothelial mesoblast is extremely well developed; according to some investigators, mesenchyme is also present.

It is worthy of note that mesenchyme is certainly phylogenetically older than mesothelium, and that those requirements which caused it to first develop may have continually recurred; so that whereas all the tissues or organs derived from mesothelium are, to a certain extent, homologous, those composed of mesenchyme may not necessarily be so.

In this connection it is interesting to note that, according to Sedgwick, at an early stage in the development of Vertebrates, most of the connective tissues of the wall of the body and gut are derived by a process of growth outwards of cells from the epithelium of the body-cavity. The same, he believes, holds good for the connective tissue and blood-vessels of the Wolffian body.

Cœlomic cavities.—Sedgwick has very recently drawn attention to the history of the cavities enclosed by mesothelial mesoblast. He finds from his researches on *Peripatus* that it is probable that throughout the Arthropoda the cavity of the body and all the vascular spaces are pseudocœlous. The lumen of the generative organs is in all cases cœlomic, as is also the nephridial apparatus of *Peripatus*. The excretory organs of other Arthropoda require re-investigation.

In Mollusca the pericardium, nephridia and possibly the ducts of the generative organs are cœlomic. The vascular system and all the lacunæ in the body are pseudocœlous.

In the Chætopoda and Chordata the cavity of the body is entirely cœlomic, and from its walls are derived the nephridia and the generative organs. The pseudocœl (archicœl) is only represented in the adult by the complicated system of vascular channels.

CHAPTER IV.

GENERAL FORMATION OF THE BODY AND DEVELOPMENT OF THE
EMBRYONIC APPENDAGES.

THE three germinal layers, the development of which has now been traced, constitute the rough material, so to speak, for the further building up of the embryo. No new formative tissue will make its appearance, and it now remains to follow the further history of these layers. Before this can be done in detail, it is necessary to gain some idea concerning the formation of the embryo as a whole, and of some of the various secondary structures which are often associated with larval or foetal life.

In all those forms possessing a small amount of food-yolk, such as the *Cœlenterata*, *Echinodermata*, most *Vermes*, a few *Mollusca*, *Amphioxus*, *Lamprey*, and *Amphibia*, the embryo has been carried to a stage which may roughly be stated to consist of an oval or rounded body with usually a single layer of epiblast. The primitive stomach or archenteron is lined with a single layer of hypoblast, and opens to the exterior by the usually posteriorly situated blastopore. The archenteron is more or less surrounded by mesoblast, which, as has just been shown, may have a single or a multiple origin.

Cœlenterata—Radial Symmetry.—The Hydroids may, in general terms, be said never to advance beyond this stage. In the fixed forms, which may be regarded as tentaculate gastrulæ, the mesoblast is merely represented by the inconspicuous structureless lamina, the gelatinous tissue of the medusoid forms with its stellate cells, clearly having relation to their mode of life. The development of many Hydroids is obscured by abbreviation.

The Actinozoa can also be briefly dismissed, but they arrive at a higher stage of evolution than the Hydrozoa. A further ingrowth of epiblast takes place at the blastopore, so that a mouth and œsophagus lined by epiblast are formed. Such an epiblastic ingrowth is known as a stomodæum. The walls of the body are

further symmetrically and bilaterally infolded. The cavity of the body (archenteron) is thus divided into a number of diverticula or pouches, separated by mesenteries, which primarily extend to the wall of the depending œsophagus. The epiblast (ectoderm) does not enter into the mesenteries.

The Actinozoa have advanced beyond the purely gastrula stage by acquiring a stomodæum and persistent archenteric diverticula. The compound and skeleton-producing forms exhibit no real advance upon this plan. Hæckel maintains that the Scyphomedusæ and Actinozoa are offshoots from a primitive branch (Scyphopolypi) of the Cœlenterata.

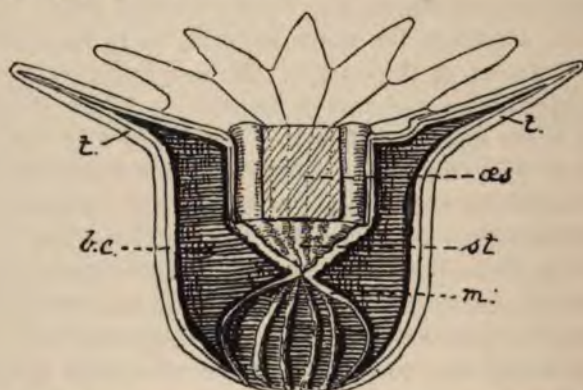


FIG. 68.—IDEAL SECTION THROUGH THE LONG AXIS OF A SEA-ANEMONE.

The sides of the mouth and œsophagus are supposed to be appressed together, leaving only the two extremities open, which, in this case, form two channels of communication with the temporary stomach.

b.c. inter-mesenterial chambers or body-cavity; *m.* edge of mesentery; *œs.* œsophagus or stomodæum; *st.* temporary stomach, formed by the contiguous upper digestive edges of the mesenteries; *t, t.* axial tentacles in longitudinal section. The mesoderm is merely represented by the line between the ectoderm and endoderm.

It is a very significant fact that, so far as is known at present, digestion takes place in the Actinozoa only by means of the enlarged edges of the mesenteries. When food is introduced into the body, the edges of the mesenteries close round it and thus form a temporary stomach, which, for the time being, is cut off from the archenteric diverticula. This "stomach" communicates with the exterior by the elongated mouth. The latter is often temporarily constricted at the sides, merely leaving an orifice at each end, which simulates a mouth and anus, as shown in fig. 68. Wilson and others, appreciating these facts, have speculated upon the possible origin of the higher Metazoa from such a primitive form.

Formation of Body-Cavity.—In the Echinodermata a distinct advance in structure is made consequent upon a free as opposed to a sessile existence. Owing, probably, to the hypoblast actually lining the wall of the body in the Actinozoa, the gastric pouches

can only be formed by ingrowths of the hypoblast and mesoblast into the archenteron. There is, however, in the Echinodermata (fig. 52) a large space, the segmentation-cavity, between the archenteron and the body-wall (epiblast now being lined by mesamœboids). Thus archenteric diverticula can be directly formed, and, being developed, can surround the archenteron. This method of forming a true body-cavity is also characteristic of all the coelomatus Metazoa, although it may be greatly modified and abbreviated. The actual formation of the body-cavity in representative examples of the Metazoa has already been briefly described.

Metamerism.—When only a single pair of archenteric diverticula are formed, the animal is, in the true sense of the term, unsegmented. But usually a considerable number of diverticula appear, either directly from the archenteron, as in *Amphioxus* (fig. 57), or indirectly from the lateral mesoblastic bands, the abbreviated but usual method (p. 56). These forms are termed segmented, and the segments may remain more or less distinct (*Chætopod Worms*) or become almost obliterated (*Vertebrates*).

The question of metameric segmentation is too intricate a one to be here discussed. It must suffice to point out that, while externally unsegmented, many *Platyhelminth Worms* have a repetition of their internal organs, especially in the case of the gastric diverticula and the generative glands. In the *Chætopoda* the body is divided into a large number of mesoblastic somites, and more or fewer of the organs may be implicated in this metamerism. In the great majority of *Arthropods* the segmentation tends to become obscured—it only affecting the exoskeleton, the appendages, the muscular system, and the nervous system.

The metamerism of the *Chordata* has many peculiar features, as several important organs are unaffected by it, and others only partially so. The neural plate and notochord always appear very early, and are from the first unsegmented. Whether primitively segmental or not, the nerves would necessarily acquire a serial position if the muscles were segmented. The segmentation of the vertebral column is unquestionably a secondary phenomenon. As Bateson points out in dealing with the ancestry of the *Chordata*, the segmentation of the gill-slits has been acquired within the group of the *Chordata*, as nothing resembling them occurs outside it. The liver is from the first a single structure (*e.g.*, *Amphioxus* upwards), and never shows any indication of having a paired

or multiple origin. Although the mesodermal segmentation of *Amphioxus* is so marked (figs. 56, 57), the metamerism of the Chordata is really very partial, and there is insufficient evidence in support of the view that the Chordata were derived from segmented ancestors; the converse proposition is perhaps more in accordance with the facts. Hubrecht has brought forward numerous arguments in favour of his belief that the Nemertean Worms and the Chordata arose from a common stock. Dohrn and Semper are the leading advocates of the Annelidan ancestry of the Chordata.

Bilateral Symmetry.—Metamerism and bilateral symmetry are the results of the progression of the animal in a determinate direction, and this also induces the development of paired ambulatory appendages and the specialisation of an anterior region or head, and conversely of a passively following region or tail.

It is as a result of the different impressions made upon them, and of their response to these stimuli, that the different regions of the body possess such marked and constant characters.

When an animal is sessile, external influences may act upon it equally in every direction, and in response to these the animal acquires a radial symmetry; but when an animal progresses in a definite direction, the two sides of the body will be subject to somewhat different conditions from those affecting the extreme anterior extremity. On the development of distinct muscles to assist in progression, the stress of the muscles would probably make the bilateral symmetry more marked. It is also evident that there would accrue a distinct advantage to the organism if the muscles were symmetrically situated and were of comparatively short length, as by this means they could act in concert or in opposition and give considerable power of motion to the animal. This is exactly the condition of the muscular somites (muscle-plates), which have already been described for numerous embryos.

Those Echinodermata which can move in any direction, such as the Starfish, have a radial symmetry, which almost completely masks their fundamental bilateral symmetry as exhibited in the embryo. Almost without exception the remaining Metazoa are entirely bilaterally symmetrical.

A far greater degree of specialisation can be reached in segmented animals, as the serial multiplication of organs gives the necessary material for concentration, as a consideration of the anterior segments of the higher Worms and the concentration and adaption which has taken place in the head and anterior region of Arthropoda will fully demonstrate.

The region in front of the stomodæum usually projects forward as the pre-oral lobe. This portion of the body, and that immedi-

ately surrounding the mouth, are collectively known as the head. From its position, the head is the seat of most of the sense-organs, and of the most specialised portion of the nervous system.

A post-anal extension of the body constitutes the tail; this very rarely exhibits any features of special interest apart from the mechanical function of propulsion, which it sometimes performs.

Paired lobes from the head or sides of the body are usually developed, which are jointed only in Arthropods. The dorsal processes on the head are usually sensory in function; when ventral cephalic appendages are present they are modified to form masticatory organs (jaws). The paired lateral appendages of the body variously serve for progression, prehension, or respiration.

It must be taken as granted that the form of any given embryo is determined by two causes, first by inheritance, and secondly by the special conditions in which it is placed. It is one of the most difficult of embryological problems to distinguish between these two, and to discover whether the larval form has any special phylogenetic significance.

The characteristic larval forms of most groups of animals are now recognised to be of such great importance that they are described in most zoological text-books, and therefore need not be here dealt with.

Fate of the Blastopore.—The fate of the blastopore is so varied as to have led to very different conceptions concerning its real nature, since the blastopore may persist as the mouth or the anus, or as both, or it may form neither.

A. Invertebrates.—Without entering deeply into controversial questions, it may be regarded as a generally received opinion that the blastopore was primitively elongated (see fig. 17). In *Peripatus* (fig. 69), which is admittedly an unspecialised form, the elongated blastopore becomes constricted in the middle, thus leaving an orifice at each end, one of which persists as the mouth and the other as the anus. Both these orifices communicate with the archenteron, and as the body elongates the apertures become widely separate, and form the terminal openings of the alimentary canal. The ventral or neural aspect of the body thus corresponds with the surface on which the blastopore occurs, the fused lips of the blastopore coinciding with the median ventral line.

As an ingrowth of epiblast usually occurs round the lips of the blastopore, the cavities of the mouth and anus are lined with epiblast. As has been previously mentioned, the oral invagination

is termed the stomodæum, and the anal is called the proctodæum. As a rule, the stomodæum and proctodæum constitute a very small portion of the alimentary canal as compared with that which is formed by the archenteron (mesenteron). In Crustacea, however, the hypoblastic portion of the alimentary canal is, as a rule, relatively very minute (fig. 140).

In Nudibranchs the elongated blastopore closes over from behind forwards, so that only the oral aperture persists (fig. 17). In the Pulmonate Mollusc *Paludina* it is the anus which remains unclosed, and in most cases when the blastopore persists it does so as the anus.

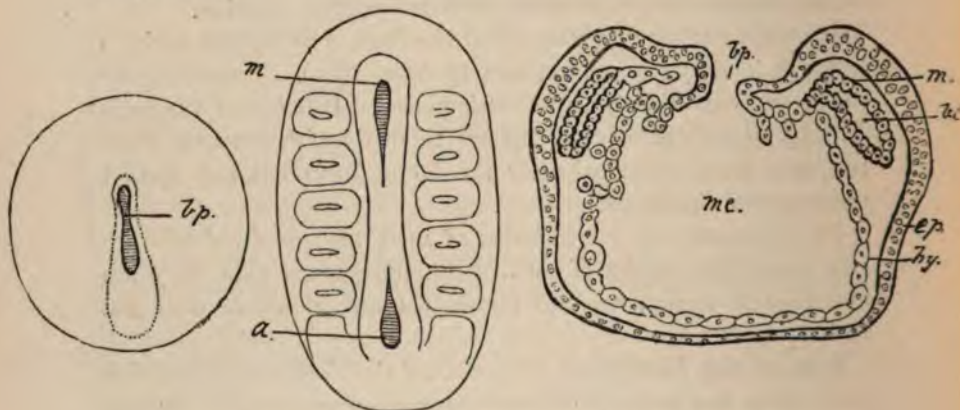


FIG. 69.—EMBRYOS OF *PERIPATUS CAPENSIS*. [After Balfour.]

A. Surface view of gastrula with elongated somewhat constricted blastopore. B. Later embryo in which the sides of the still more elongated blastopore have grown together; five mesoblastic somites are present. C. Transverse section through the blastopore of the last.

a, anus (proctodæum); b.c. body-cavity (coelom); bp. blastopore; ep. epiblast; hy. hypoblast; m. mouth in B, mesoblastic somite in C; mc. mesenteron.

Chordata.—The relation of the mouth and the anus of the Chordata to the blastopore is a problem which is at the present time receiving considerable attention.

The belief, however, is gaining ground that the neural aspect of the body in Vertebrates is identical with that of Invertebrates; in other words, the terms dorsal and ventral have opposite meanings as ordinarily applied in these two groups.

An ancestral form of the Chordata may be conceived as having been an elongated animal with a mouth and anus which were the persistent terminal orifices of the elongated blastopore. The body was produced in front of the mouth into a pre-oral lobe, but the anus was situated at the extreme hinder end of the animal. The segmented body-cavity was derived from archenteric diverticula, as is now the case

in *Amphioxus*. The nervous system was differentiated from the external skin, and, being derived from a nervous ring round the primitive blastopore, consisted of a ventral plate mainly situated between the mouth and the anus; the symmetrical halves of which it is composed would result from the junction of the lips of the blastopore. In front of the mouth the neural plate was greatly enlarged in connection with the specialisation of the pre-oral lobe to form the brain, on which the pit-like eyes were situated (fig. 139).

The folding over of the neural plate to form a neural tube greatly diminished the facility of the communication of the archenteron with the exterior. In the larval *Amphioxus* the archenteron for a long time opens into the posterior end of the neural canal, through what is known as the neurenteric canal (fig. 57), the neural canal itself opening to the exterior by an anterior pore. But the anterior region of the archenteron (pharynx) communicated with the exterior by means of the developing gill-slits; and it is assumed by Dohrn and others that an anterior pair of gill-slits gradually became modified to form the vertebrate mouth. Sedgwick, however, believes that the mouth is homologous all through the Metazoa, and that it always retains its original position at the anterior end of the true primitive blastopore.

Most embryologists consider the anus of Vertebrates to be a new structure, but Sedgwick regards it as the posterior extremity of the primitive blastopore. In the Lamprey, and several Amphibia, the blastopore is stated to remain permanently open, and to persist as the anus. Weldon describes the proctodæum in the Lizard as arising within the region of the primitive streak. If the second view be established, it follows that, as in many Invertebrates, the anus of the Chordata assumes a secondary position on the opposite, abneural, side of the body to its place of origin, owing to the elongation of the body. This prolongation constitutes the tail of the Chordata, see figs. 98, 99, which illustrate this for the Frog.

It has been further supposed by Cunningham that the neural plate of the primitive Chordata was folded along the median line, so as to form a groove into which the primitive mouth and anus opened. By this time the anterior region of the archenteron was perforated by paired slits, forming the characteristic respiratory pharynx of the group.

The primitive mouth opened into the archenteron near the anterior extremity of the neural plate. The folding over of the latter to form the neural canal would render the former useless, and a pair of gill-slits are supposed to have assumed its function. Cunningham suggests that the infundibulum (see p. 110) is the remnant of the primitive mouth, a view which he maintains is supported by the relations of that diverticulum.

The invagination of the neural plate caused the eyes, which appear to have been simple pit-like depressions of the pre-oral lobe, to develop as outgrowths from the anterior region of the brain (fig. 139); the relative position of the ganglionic to the retinal layer of the optic vesicle entirely supports this conclusion. An account of the development of the eye will be given later (p. 157). Other sense-organs were developed according to the requirements of the animal.

The limbs of Vertebrates are now usually considered to be specialisations of a primitively continuous lateral ridge or fin.

Accepting the interpretation given above of the homology of the Vertebrate embryo, the following fusions of the embryonic layers must be supposed to occur (see fig. 62).

1. The fusion of the lips of the primitive blastopore, extending from the primitive mouth to the primitive anus, a region which roughly corresponds with the neural plate. Miss Johnson has described a primitive groove and a primitive streak with the fusion of the layers in this region in the Newt.
2. The union of the lips of the blastoderm behind the embryo in telolecithal ova, forming the "primitive streak" of most authors.
3. The junction of the edges of the blastoderm as they unite after extending over the yolk.

Free Larvæ.—Embryos may commence a free existence in practically any stage of development, though the age at which an embryo is hatched or born is definite for the species, if not for the group.

Those forms which commence their free existence at an early stage of development possess many larval structures and organs to enable them to hold their own in the struggle for existence. During their further life-history they pass through regular stages of development, which are usually attained by gradual growth; but in some cases (*e.g.*, Arthropoda) the changes are hurried over during moults of the skin. Speaking generally, alecithal ova are soonest hatched.

The acquirement of food-yolk is associated with a prolongation of pre-natal existence, but the tendency to undergo a metamorphosis still persists. Consequently rudimentary organs occur during development which receive their explanation in the loss of a free larval life, and even moultings of the skin may occur.

In Vertebrates higher than the Amphibia (Amniota) certain foetal appendages are developed, which must now be considered.

Foetal Membranes of Birds.—The following account of the embryonic appendages refers to the Fowl, but doubtless it is equally applicable to other Birds.

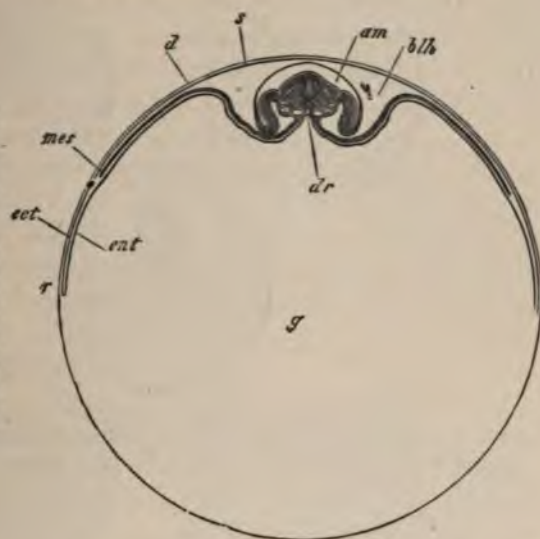
Owing to the large amount of yolk present in the ova of Birds the embryonic area is relatively small. At first the germinal disc is flat, but soon the anterior extremity of the embryo is limited by a fold in the area pellucida, which is known as the head-fold, and, as was described on p. 39 (fig. 72), the embryo is gradually constricted off from the yolk, which is henceforth known as the yolk-sac (umbilical vesicle of Mammals).

The middle germinal layer (mesoblast) early splits into two layers; the outer layer unites with the epiblast to form the somatopleur or body-wall and the inner unites with the hypoblast and constitutes the somatopleur. The space thus produced, and which is surrounded by the mesoblast, is the future body-cavity (coelom), but it is often termed the pleuro-peritoneal cavity, as being the cavity which encloses the lungs and abdominal viscera; as will be subsequently described, the lungs come to be enclosed in a special portion of the coelom. The splitting of the mesoblast first occurs in the embryonic area, but as the mesoblast extends farther and farther round the yolk, it continues to split, as will be seen in figs. 70–75. Thus when the mesoblast entirely surrounds the yolk-sac (fig. 72, F and G; 75, D), the latter really lies within

the body-cavity (pleuro-peritoneal cavity) of the embryo. By this time the yolk-sac is greatly reduced in size owing to the absorption of the yolk by the hypoblast and blood-vessels of the area vasculosa, and ultimately it dwindles away.

FIG. 70.—TRANSVERSE SECTION OF AN EMBRYO FOWL OF THREE DAYS' INCUBATION. The size of the embryo is exaggerated. [From Kölliker.]

am, amniotic cavity; bla, extension of the pleuro-peritoneal cavity outside the embryo; d, vitelline membrane; dr, cavity of the mesenteron; ect, epiblast; ent, hypoblast; g, yolk; mes, border of the splanchnic mesoblast (area vasculosa); r, edge of the blastoderm, here consisting only of epiblast and hypoblast; s, serous or subzonal membrane.



Amnion.—About the twentieth hour of incubation of a Fowl's egg a semilunar fold of the blastoderm appears in front of the future anterior extremity of the embryo (fig. 33). This fold, which

FIG. 71.—DETAILS OF THE EDGE OF THE MESOBLAST OF A FOWL'S OVUM ABOUT THE STAGE OF FIG. 70. [After Duval.]

ep, epiblast; hy.n, free nuclei in the yolk, which will give rise to the hypoblast of the yolk-sac; pp, pleuro-peritoneal cavity or celom; so.m, somatic mesoblast; sp.m, splanchnic mesoblast; y, yolk.



is a reduplication of the somatopleur, is the anterior fold of the amnion. Somewhat later a second fold makes its appearance behind the posterior extremity of the embryo; this unites with the

anterior fold through the production of lateral folds, and the embryo lies in a shallow depression bounded by the amniotic fold. The folds now increase in size (fig. 72, A, D, B), and soon unite in



FIG. 72.—DIAGRAMS TO ILLUSTRATE THE DEVELOPMENT OF THE AMNION AND ALLANTOIS.
[From Bell, after Foster and Balfour.]

In A the embryo (*e*) is being constricted off from the yolk-sac, and the folds of the amnion are to be seen rising up at either end of the embryo, the anterior fold (*af*) being the larger; in B the amniotic folds nearly meet, and in C they have entirely coalesced. In D, which is a little later stage than A, the allantois (*al*) is budding out from the intestine; in E, which is a stage corresponding with C, the allantois is seen extending round the embryo. In F the yolk-sac (*y*) is reduced in size, and in G it is being withdrawn into the body of the embryo. The allantois in F and G is omitted for the sake of simplicity.

These diagrams only very roughly indicate the relations of the parts. In all the embryo is represented by horizontal shading, the pleuro-peritoneal cavity is dotted, and the yolk-sac has concentric lines. The dotted line indicates the vitelline membrane.

the median line above the embryo; their walls coalesce, and finally break down at the points of apposition, so that the enclosed cavity becomes continuous (figs. 72, C, E, and 79, 2, 3, 4).

The closure of the amniotic orifice by the fusion of the folds takes place from before backwards, till, at the commencement of the third day, a small opening is left over the tail, which then closes over.

The inner membrane of the amnion (amnion proper) thus forms a complete sac round the embryo (figs. 70-83), and the enclosed space is the cavity of the amnion containing the liquor amnii. The outer amniotic membrane (false amnion or serous membrane) lies immediately below the vitelline membrane.

The space between the true and the false amnion, as will be clearly seen on reference to figs. 70-79, is merely an extension of the body-cavity or cœlom (pleuro-peritoneal cavity). It is everywhere bounded externally by the somatopleur, and internally by the splanchnopleur, which invests the yolk (fig. 72, B

FIG. 73.—FORMATION OF THE ALLANTOIS. Longitudinal section of the posterior extremity of an embryo Fowl of the third day. Osmic acid preparation strongly contracted by the reagent. [From Kölliker.] Magnified 150.

al, rudiment of the allantois; *am*, amnion; *cl*, cloaca; *d*, posterior border of the intestino-umbilical orifice; *d'*, rectum; *dg*, splanchnopleur, where the intestinal wall passes round the yolk, thus forming the anterior border of the tail-fold; *s*, posterior extremity of embryo.



and E). The body-cavity is thus gradually extending below the yolk-sac at F (fig. 72), the two sides have met, and have quite coalesced in G.

Allantois.—During the formation of the folds of the amnion a sac projects from the splanchnopleur of the hind-gut into the body-cavity. This is the allantois; it is lined internally with hypoblast (figs. 72-75). The allantois grows rapidly, extending all round the embryo in the space enclosed by the false amnion.

The further history of the allantois in Birds has recently been carefully studied by Duval. He finds that the outer membrane of the allantois fuses with the serous membrane, or, as it is preferable to call it, the subzonal membrane. (The compound tissue thus formed consists of an outer epiblastic epithelium, a middle layer produced by the fusion of the mesoblast of the subzonal membrane (somatic mesoblast) with that of the allantois (splanchn-

nic mesoblast), and an inner epithelium, the hypoblastic lining of the allantois, fig. 74, B).

Instead of remaining, as it were, within the confines of the body-cavity of the embryo, the allantois protrudes beyond the inferior margin of the yolk-sac, of course carrying the subzonal membrane with it (fig. 75, A, B).

The inferior folds of the allantois enclose the albumen and meet one another below the embryo (fig. 75, C). They next considerably overlap each other, and eventually fuse together (fig. 75, D).

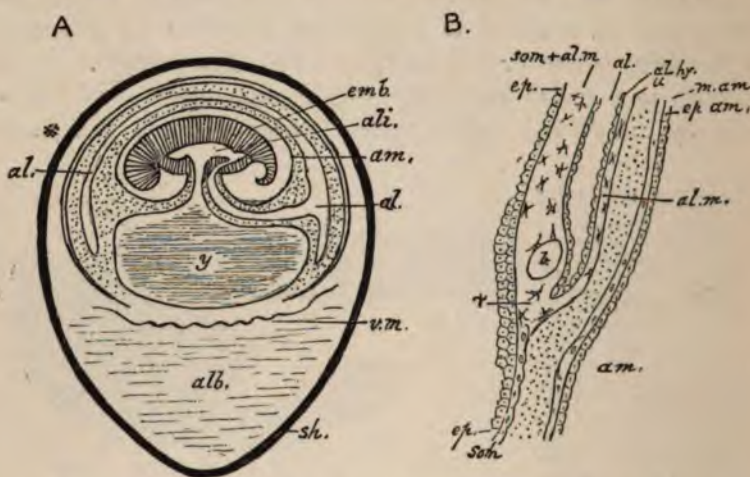


FIG. 74.—A. DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE EGG OF A FOWL.
B. DETAIL OF A PORTION OF THE SAME AT A TIME WHEN THE ALLANTOIS
REACHED THE SPOT MARKED X IN A. [After Duval.]

al. cavity of allantois; alb. albumen; ali. mesenteron; al.hy. hypoblastic epithelium of allantois; al.m. mesoblast of allantois; am. cavity of amnion; b. blood-vessel; emb. embryo; ep. epiblast of outer layer of amnion (serous membrane); ep.am. epiblastic epithelium of inner layer of amnion (amnion proper); m.am. mesoblastic layer of latter; sh. egg-shell; som. somatic mesoblast of outer layer of amnion; v.m. vitelline membrane; † point where the mesoblastic tissue of the allantois fuses with that of the serous membrane.

The remaining albumen of the egg is thus enclosed in a space bounded above by the ventral wall of the yolk-sac, and below by the folds of the allantois. This space is termed by Duval the placental sac. Simple villi grow out from the epiblast lining the placental sac to absorb the contained albumen, the nutriment being conveyed to the embryo by the blood-vessels of both the yolk-sac and the allantois.

It is interesting to note that at first villi arise from the epiblast of the inferior pole of the yolk-sac (fig. 75, A, B). Later they are developed from that portion of the non-embryonic epiblast which

is lined by the allantois; in other words, from a true chorion (see p. 90).

The cavity of the amnion gradually extends all round the em-

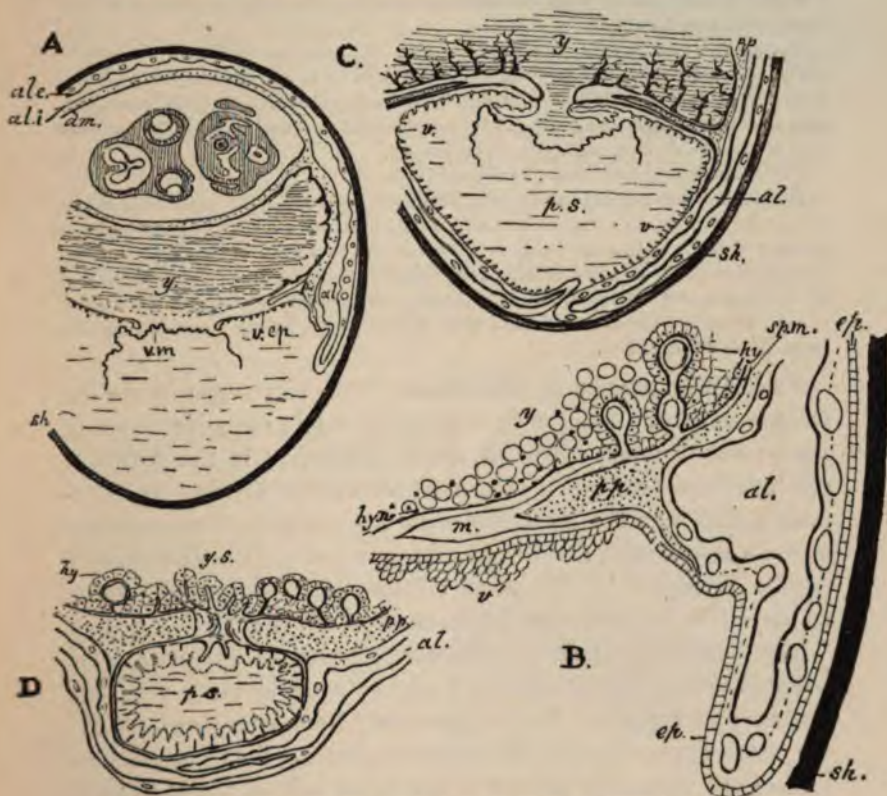


FIG. 75.—DIAGRAMS ILLUSTRATING THE FORMATION OF THE PLACENTAL SAC IN BIRDS.
[After Duval.]

A. Section of an egg of a Warbler ("Fauvette") corresponding to that of a Fowl from the eighth to the tenth day. B. Detail of a portion of the above. C. Ventral portion of an egg of the same, corresponding to that of a Fowl about the fifteenth day. The two allantoic culs-de-sac have come into contact, forming a placental sac with internal villi. D. Diminished placental sac of the same, shortly before hatching.

al. cavity of allantois, the thick line in B-D indicates its hypoblastic epithelium; alc., ali. outer and inner layers of the allantois; am. amnion; ep. epiblast of serous or sub-zonal membrane,—the dotted line between the epiblast and the hypoblast of the allantois indicates diagrammatically the distinction between the mesoblast of the serous membrane and that of the allantois; hy. hypoblast surrounding the yolk,—the folds of the hypoblast enclose blood-vessels which have been developed from the splanchnic mesoblast; hy.n. free nuclei which will form the vitelline hypoblast; m. unsplit mesoblast; p.p. extra-embryonic body-cavity (pleuro-peritoneal cavity); p.s. placental sac; sh. egg-shell; sp.m. splanchnic mesoblast; v. epiblastic villi of placental sac; v.m. vitelline membrane; y. yolk.

bryo, but for some time leaves a narrow pedicel surrounding the stalks of the yolk-sac and allantois (fig. 72, G, the latter is omitted in this fig., and figs. 79, 5; 83). This pedicel is known in Mammals

as the umbilical cord. In Birds it ruptures just before hatching after the withdrawal of the yolk-sac into the body-cavity of the embryo. In Mammals it is only severed after birth.

Fœtal Membranes of Reptiles.—Our knowledge of the fœtal membranes of Reptiles is still very imperfect.

The amnion first appears as a hood covering that anterior portion of the embryo which very early sinks into the yolk-sac. The anterior fold of the amnion consists of both epiblast and somatic mesoblast, and it gradually extends backwardly in conjunction with lateral folds which arise along the sides of the neural plate. The posterior fold of the amnion does not appear to be present.

The allantois probably resembles that of Birds.

Haacke has shown that in the Lizard *Trachydosaurus asper* the egg-shell is absent except for a small disc-shaped rudiment which lies between the yolk-sac and the uterus; thus the embryo is readily seen through the thin walls of the uterus and the transparent embryonic membranes. This Lizard is viviparous, and the vascular wall of the yolk-sac is only separated from the special capillary network of the uterine vessels, which is concerned in the nutrition of the embryo, by the porous and friable rudiment of the egg-shell.

Fœtal Membranes of Mammals.—The early stages in the development of the embryo in Mammals closely resemble those of Birds; but there are a few important differences in the nature of the fœtal membranes. The differences are mainly due in Mammals higher than the Monotremes to the absence of an egg-shell with its membranes, and of the albumen and yolk. The ovum is merely protected by the zona radiata (zona pellucida), within which a delicate membrane has been observed (fig. 5).

The hollow yolk-sac or blastodermic vesicle grows rapidly; being distended by a contained fluid, the zona becomes very thin and early disappears. As has previously been mentioned (p. 45), the germinal area alone of the oosperm possesses the three germinal layers; the remaining portion of the upper half of the oosperm is lined with epiblast and primitive hypoblast, whereas the lower half of the blastodermic vesicle is composed solely of epiblast (fig. 42).

Simple non-vascular villi, which serve to attach the embryo to the walls of the uterus, usually project from the epiblast of the blastodermic vesicle (subzonal membrane). In the Rabbit they only occur on that area of the epiblast under which the mesoblast will not extend (figs. 77, 78), with the exception of a horse-shoe shaped patch which early makes its appearance in the region of the future placenta, and with which it shortly becomes identified (fig. 76, *pl*).

The following account of the development of the amnion is taken from Van Beneden and Julin's recent researches on the development of the Rabbit.

Pro-amnion.—The mesoblast (fig. 76, *a.v.*) extends for some distance from the embryo in every direction, except immediately around the head; but the two limbs of mesoblast which bound this emargination gradually extend round some distance in front of the head and eventually unite (fig. 76). Thus it comes about that there is a nearly circular area in front of the head in which the blastoderm consists of epiblast and hypoblast only.

This area early sinks into the cavity of the blastodermic vesicle, and the anterior extremity of the embryo projects into this depression, which Van Beneden and Julin term the pro-amnion (figs. 76-78, *p.am.*).

Amnion.—Very slightly later the true amnion is developed, but only over the posterior end of the embryo (figs. 76, 77). It

FIG. 76.—DIAGRAMMATIC DORSAL VIEW OF AN EMBRYO RABBIT WITH ITS MEMBRANES AT THE STAGE OF NINE SOMITES. [Modified from Van Beneden and Julin.]

al. allantois, showing from behind the tail fold of the embryo; *am.* anterior border of true amnion; *a.v.* area vasculosa, the outer border of which indicates the farthest extension of the mesoblast; *bl.* blastoderm, here consisting only of epiblast and hypoblast; *a.m.v.* omphalo-mesenteric or vitelline veins; *p.am.* pro-amnion; *pl.* non-vascular epiblastic villi of the future placenta; *s.t.* sinus terminalis.



rapidly grows forwards until it comes in contact with the raised anterior rim or fold of the pro-amnion, with which it fuses. The cavity of the amnion coalesces with the space (extra-embryonic pleuro-peritoneal cavity) resulting from the splitting of the mesoblast, which now extends in front of the embryo and the pro-amnion.

In process of time the pro-amnion gradually atrophies, and the true amnion correspondingly advances forwards.

It is now generally admitted that the amnion was primitively caused by the embryo sinking into the yolk-sac by its own weight. The protection to the embryo by the formation round it of what is virtually a water-sac resulted in the precocious development of the amnion before the embryo in its ontogeny had any appreciable weight.

The pro-amnion probably originated from a similar bearing-down of the heaviest

(anterior) end of the embryo, when the blastoderm of that region was still diploblastic (two-layered). The pro-amnion is, in fact, an exaggeration of the head-fold.

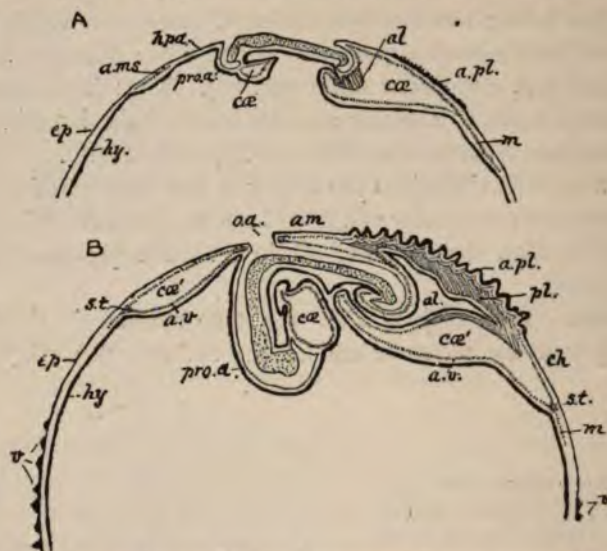


FIG. 77.—DIAGRAMMATIC MEDIAN VERTICAL LONGITUDINAL SECTIONS THROUGH THE EMBRYO RABBIT. [After Van Beneden and Julin.]

A. Section through embryo of fig. 76. B. Section through embryo of eleven days. *al.* allantois; *am.* amnion; *a.ms.* anterior median plate of mesoblast, formed by the junction of the anterior horns of the area opaca; *a.pl.* area placentalis; *a.v.* area vasculosa; *ch.* chorion; *cae.* coelom of embryo; *cae'.* extra embryonic portion of the body-cavity; *ep.* epiblast; *hy.* hypoblast; *m.* unsplit mesoblast; *a.a.* orifice of amnion; *pl.* placenta; *pro.a.* proamnion; *st.* sinus terminalis; *v.* epiblastic villi of blastodermic vesicle.

Van Beneden and Julin affirm that it not only occurs in Rodents, but also in Bats and the Dog, and that it probably exists for a short period in the Fowl and in Lizards.

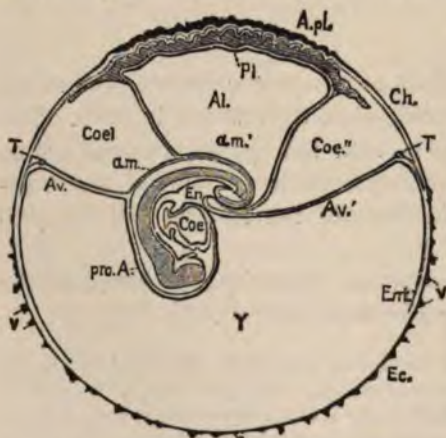


FIG. 78.—FETAL ENVELOPES OF A RABBIT EMBRYO. [From Minot, after Van Beneden and Julin.]

Later stage than fig. 77, B. The amnion has become fused with the blastoderm in front of the embryo, and its cavity is therefore continuous with the extra-embryonic portion of the body-cavity in front of the embryo.

Al. allantois; *am.* amnion; *am'.* portion of the amnion united with the walls of the allantois; *A.pl.* area placentalis; *Av.* area vasculosa; *Ch.* chorion; *Co.* coelom or body-cavity; *cae'.* extra-embryonic portion of the body-cavity; *Coel.* anterior portion of the same, produced by the fusion of the cavity of the amnion with that of the anterior portion of the area opaca; *Ec.* epiblast; *En.* alimentary canal of the embryo; *Ent.* hypoblast; *Pl.* placenta; *pro.A.* proamnion; *T.* sinus terminalis; *V.* villi of blastodermic vesicle; *Y.* cavity of blastodermic vesicle.

It would appear, therefore, that the pro-amnion is a structure which is common to a greater or less extent to the Sauropsida and Mammalia.

The anterior fold of the true amnion is certainly absent in the Rabbit, and this may prove to be the case for Mammals generally, now attention has been drawn to the question. At all events, the posterior fold of the amnion is always well developed.

By this time the partially vascular yolk-sac has gradually diminished in size; and the vascular allantois is greatly increasing in size and importance, and is functionally replacing the yolk-sac.

Allantois.—The Mammalian allantois has a similar origin to that in Birds (figs. 77, 79). It extends to a greater or less extent between the amnion and the serous membrane or subzonal membrane.

The outer membrane of the highly vascular allantois fuses, as in Birds, with the subzonal membrane, the villi of which become vascular and usually grow more complex. The compound membrane thus formed is known as the chorion. That portion of the chorion which enters into immediate connection with the uterus of the mother constitutes the foetal portion of the placenta.

As will be shown later (p. 259), the proximal portion of the stalk (urachus) of the allantois persists as the urinary bladder, and it is generally admitted that the urinary bladder (urocyst) of Amphibia is a homologous organ with that of the Amniota. It is thus a fair assumption to make that the allantois is merely the precociously developed urinary bladder.

In the lower Vertebrates the egg is usually laid in water, and the larva is, as a rule, early hatched, respiration being effected by gills situated on the gill-arches.

In *Alytes* and *Notodelphis ovipara* and some other Anura, large external gills are developed while the embryo is still within the egg-covering, their function apparently being to give increased facility for respiration to the unhatched young. A similar condition also occurs in some Elasmobranchs.

Certain Anura, however, have such an abbreviated larval existence that the young are hatched as small Frogs, and in some of these the external gills atrophy early (*Pipa americana*), or are said to be entirely absent (*Rhinoderma darwini*, *Nototrema marsupiatum*). In *Pipa* the long tail of the tadpole functions as a respiratory organ [Peters], and the same holds good for *Hylodes*. Boulenger finds that the abdomen of the just-hatched *Rana opisthodon* is provided with a lateral series of symmetrical folds, which probably have a respiratory function.

The above facts tend to show that some Frogs are losing their ancestral larval breathing organs, and are utilising other organs for respiratory purposes; and it is very significant that this occurs amongst those Frogs which do not deposit their eggs in water. It is then not difficult to imagine that some primitive Amphibian which had acquired an increase of food-yolk (as a few recent Anura have done) would find in the urinary bladder an organ which could be pressed into the service of aerial respiration.

If we may assume that some such Amphibian was the ancestor of the Amniota, we have a clue to the significance of the total absence of even rudimentary gill-filaments on the gill arches of even the youngest embryos of the less specialised Amniota in

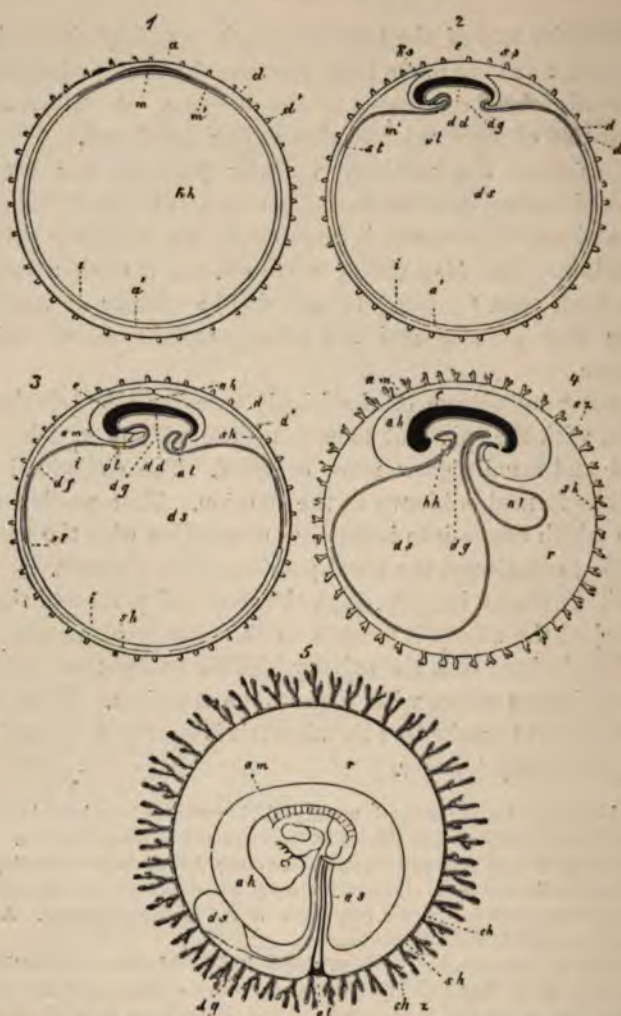


FIG. 79.—FIVE DIAGRAMMATIC FIGURES ILLUSTRATING THE FORMATION OF THE FETAL MEMBRANES OF A MAMMAL. [From Kölliker.]

In 1, 2, 3, 4, the embryo is represented in longitudinal section.

1. Oosperm with zona pellucida, blastodermic vesicle, and embryonic area. 2. Oosperm with amnion about to close and commencing allantois. 3. Oosperm with villous subzonal membrane, larger allantois, and mouth and anus. 4. Oosperm in which the vascular mesoblast of the allantois has extended round the inner surface of the subzonal membrane, and united with it to form the chorion; the cavity of the allantois is aborted. The yolk-sac (umbilical vesicle) has greatly diminished. The large amniotic cavity surrounds the umbilical cord. This fig. represents an early human ovum.

a. epiblast of embryo; *a'* epiblast of non-embryonic part of the blastodermic vesicle; *ah.* cavity of the amnion; *al.* allantois; *am.* amnion; *as.* amniotic sheath round the umbilical cord; *ch.* chorion; *ch.z.* villi of chorion; *d.* zona pellucida (radiata); *d'* processes of zona; *dd.* embryonic hypoblast; *df.* area vasculosa; *dg.* stalk of yolk-sac; *ds.* yolk-sac (umbilical vesicle); *e.* embryo; *hh.* pericardial cavity; *i.* non-embryonic hypoblast; *kh.* cavity of the blastodermic vesicle, which practically is equivalent to the yolk-sac; *ks.* head-fold of amnion; *m.* embryonic, *m'* non-embryonic, mesoblast; *r.* space between chorion and amnion containing albuminous fluid; *sh.* subzonal (serous) membrane; *st.* sinus terminalis; *sz.* subzonal villi; *vt.* ventral body-wall in the region of the heart.

the supposition that the loss of larval gills was a pre-amniote character. This was rendered possible before the lungs were functional in ontology by the acquisition of an accessory respiratory organ; in this case it was the thin-walled vascular urinary bladder. The adoption of this organ for respiratory purposes causes it to grow enormously in size, and at the same time to appear earlier. Hence the great development it now attains.

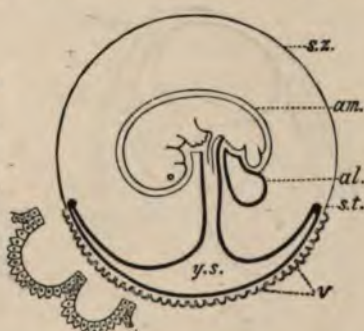
It has just been shown that in Birds the epiblast which underlies the yolk-sac is produced into villi (fig. 75, B, *v*), which absorb the nutritive albumen before the allantoic villi are developed. The same also occurs in the lower Mammalia.

In the Virginian Opossum (*Didelphys*), according to Osborn, when the allantois is still very small, the yolk-sac is provided with simple vascular villi (fig. 80, *v*), which, in addition to serving to attach the embryo to the uterine wall, are undoubtedly nutritive in function. In these Mammalia there is no albumen to feed

FIG. 80.—DIAGRAM OF THE FETAL MEMBRANES OF THE VIRGINIAN OPOSSUM. [After Osborn.]

Two villi are shown greatly enlarged. The processes of the cells, which have been exaggerated, doubtless correspond to the pseudopodia described by Caldwell.

al. allantois; *am.* amnion; *st.* sinus terminalis; *sz.* subzonal membrane; *v.* villi on the subzonal membrane in the region of the yolk-sac; *ys.* yolk-sac. The vascular splanchnopleur (hypoblast and mesoblast) is indicated by the black line.



upon, but better nutriment can be directly obtained by osmosis from the mother.

Caldwell has shown that in the Native Bear (*Phascolarctos cinereus*) (fig. 81) the inferior non-vascular moiety of the yolk-sac is, even up to a comparatively late period, surrounded only by hypoblast and the non-embryonic epiblast (subzonal membrane). The cells of the latter send out pseudopodia (fig. 81, *amb*), which fit in between the cells of the uterine epithelium. Although the allantois is larger than in the preceding form, and comes into contact with the subzonal membrane, no villi are formed by it; in other words, in the Marsupials the true chorion, if present, is rudimentary, and, so far as is known, never develops villi. The previous researches of Owen point to the same conclusion.

From the nature of the case, no adhesion occurs between the embryo and the parent in the Prototheria, any more than in Sauropsida. In the Metatheria a very slight connection does

occur, but in this union the subzonal membrane surrounding the yolk-sac alone takes part. As the latter was the sole nutritive organ of the embryos of the earlier Mammals, it would probably but slowly part with this function.

Ryder has suggested that the degeneracy of the yolk in the Mammalian oosperm may be due to the development of the so-called uterine milk from the uterine glands, and it subsequently completely disappeared in consequence of the perfectly parasitic connection temporarily subsisting between the mother and the embryo. (The latter supposition was first put forward by Balfour.) At this stage of evolution the allantois was respiratory, as it practically is in the Sauropsida, Monotremes, and Marsupials, and the yolk-sac was becoming less nutritive in function.

As the allantois is used in Birds to absorb the albumen, so in the higher Mammals (Eutheria) it develops villi where it is fused with the subzonal membrane, and forms the chorion.



FIG. 81.—DIAGRAM OF THE FETAL MEMBRANES OF THE NATIVE BEAR. [After Caldwell.]

al. allantois; am. amnion; amb. amniotic processes of the subzonal epiblast in the non-vascular region of the yolk-sac; hy. hypoblast of the non-vascular region of the yolk-sac; st. sinus terminalis; s.z. subzonal membrane; y.s. yolk-sac. The black line indicates the vascular splanchnopleur (hypoblast and mesoblast). A greatly magnified portion of the ventral wall of the yolk-sac is also given.

The term chorion is now limited to those areas of the subzonal membrane to which the yolk-sac or the allantois are attached. Balfour distinguished the former of these as the false and the latter as the true chorion. In the Rabbit (fig. 82) the false chorion is very large, and the true (or placental) chorion relatively small; but in most Mammals the true chorion has a much greater extension.

It is possibly owing to the large size of the yolk-sac that the allantois forms such a small chorion in the Rabbit. There is a remarkably close resemblance between the general disposition and structure of the fetal membranes in the Rabbit (figs. 78, 82) and some Marsupials (figs. 80, 81). In both, the epiblast (subzonal

membrane) of the yolk-sac (blastodermic vesicle) gives rise to non-vascular villi only in the region where the mesoblast has not extended. The allantois also unites with the subzonal membrane above the embryo to a small extent; but in the Rabbit vascular villi are developed at this spot, which thus form a true placenta.

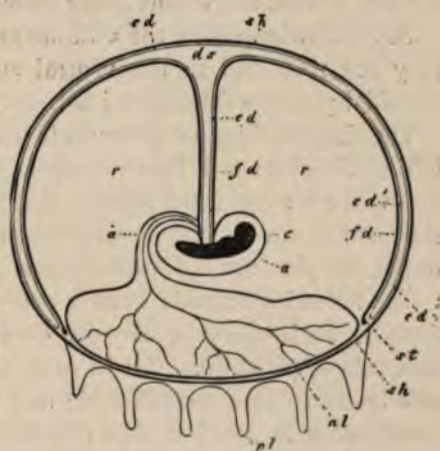
The epiblast of the blastodermic vesicle appears to give rise to villi in other Mammals, but more precise information is required on this point.

The nature and position of the villi of the chorion vary considerably. The villi fit into depressions of crypts of the uterine wall, the conjoint structure being known as the placenta.

The placenta of the Rodentia, Insectivora, and Chiroptera is usually dorsally situated and discoidal, as in the Rabbit, and is

FIG. 52.—DIAGRAMMATIC LONGITUDINAL SECTION OF OOSPERM OF RABBIT AT AN ADVANCED STAGE OF PREGNANCY. [From Kölliker after Bischoff.]

a. amnion; al. allantois with its blood-vessels; c. embryo; ds. yolk-sac; ed, ed', ed'', hypoblastic epithelium of the yolk-sac and its stalk (umbilical vesicle and cord); fd. vascular mesoblastic membrane of the umbilical cord and vesicle; pl. placental villi formed by the allantois and subzonal membrane; r. space filled with fluid between the amnion, the allantois, and the yolk-sac; st. sinus terminalis (marginal vitelline blood-vessel); u. urachus or stalk of the allantois.



co-extensive with the area of contact between the allantois and the subzonal membrane. In these forms the yolk-sac is in contact with the larger portion of the subzonal membrane.

In Edentata the placenta may be discoidal (Loricata), or dome-shaped (Pilosa), or zonary (Tubulidentata), that is, occupying a broad band round the chorion, leaving the ends free from villi, or diffuse (Squamata).

In the Dog the large vascular yolk-sac does not fuse with the subzonal membrane. The allantois first grows out on the dorsal side of the embryo, where, coalescing with the subzonal membrane, it forms an at first discoidal placenta. The villi soon extend, so as to form a zonary placenta. The zonary placenta is found in the Carnivora, Hyrax, and Elephas.

The extension of the placenta over the whole of the chorion results in what is termed a diffused placenta; this is characteristic of the Perissodactyla, the Suina, the Tragulina, the Tylopoda, the Sirenia, the Cetacea, the Lemuroidea.

The collection of the villi into groups constitutes what is known as a cotyledonary placenta. This variety is confined to the Pecora. In the Giraffe, the placenta is partly diffused and partly cotyledonary. Weldon finds that in the Four-horned Antelope (*Tetraceros*) the whole surface of the chorion is thrown into vascular ridges, exactly as in the Pig, and the cotyledons are very few in number (twenty to thirty), other Antelopes having sixty or more. The Bovidae possess a large number of cotyledons, while the Cervidae have only a very few. In *Moschus*, however, the placenta is finely folded, cotyledons being absent.

In the Anthropeidea, the villi are at first diffuse, but ultimately they are restricted to the ventral surface, forming a secondary discoidal placenta (metadiscoidal).

The simplest kind of placenta is one in which the papilla-like villi of the chorion fit into corresponding depressions in the uterus. The villi are ranged in irregular ridges in the Pig. In such forms the chorion can be withdrawn at birth from the placenta; in other words, the placenta is non-deciduate.

The following animals have a non-deciduate placenta:—Artiodactyla, Perissodactyla, Sirenia, Cetacea, Lemuroidea, and some Edentata (Squamata). But in some of these the villi are more or less branched and complicated; and in many of the Pecora this interlocking is so close that the parts of the epithelium of the maternal cotyledons may be carried away at birth.

In all the other Eutheria the foetal villi are so intimately connected with the uterine wall, that at birth a greater or less portion is brought away with the allantois (after-birth). This form of placenta is known as the deciduate.

The uterus merely develops short tubular crypts to surround the foetal villi in the case of those Mammals with a simple non-deciduate placenta. But in those with a deciduate placenta the wall of the uterus undergoes varied structural modifications, which reach their extreme form in the Anthropeidea, where the foetal villi are immersed in large uterine blood-sinuses.

Very shortly after the human ovum has entered the uterus, the walls of the latter grow round and incapsulate it (fig. 83). The reflected portion of the uterus is called the decidua reflexa. That

portion of the wall to which the embryo is attached is known as the decidua serotina, the decidua vera being the remaining surface of the uterus. All these structures are cast off in the act of birth.

The decidua reflexa is more or less developed in a few other Mammals, *e.g.*, Seals, and some Insectivora.

Inversion of Germinal Layers in Rodents.—A peculiar inversion of the germinal layers in the blastoderm of the Guinea-pig was first described by Bischoff, and later confirmed by Hensen and Schäffer. Four papers were simultaneously published at the end of the year 1882, in each of which there was practically an identical solution

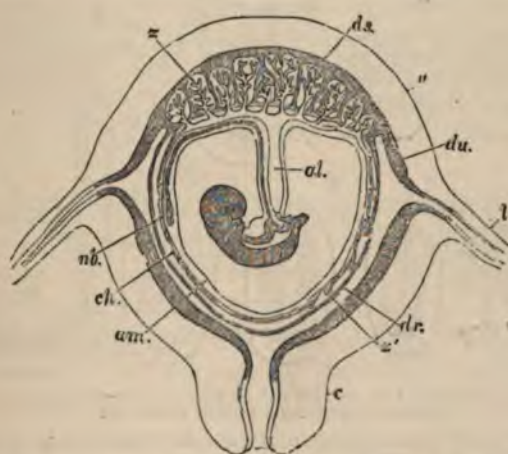


FIG. 83.—DIAGRAMMATIC SECTION OF PREGNANT HUMAN UTERUS, WITH CONTAINED FETUS. [From Huxley after Longet.]

al. allantoic stalk (urachus); *am.* amnion; *c.* cervix uteri; *ch.* chorion; *dr.* decidua reflexa; *ds.* decidua serotina; *dv.* decidua vera; *l.* Fallopian tube (oviduct); *nb.* umbilical vesicle or yolk-sac; *z.* foetal villi of the true placenta; *z'* villi of the non-placental part of the chorion.

The portion of the uterine wall to which the embryo is attached is the decidua serotina; that portion which grows round the embryo is the decidua reflexa, while the general wall of the uterus, not related to the embryo, is the decidua vera.

of this difficult problem. The forms studied were the Field-vole (*Arvicola arvalis*) by Kupffer, the House-mouse (*Mus musculus*) by Selenka, the Guinea-pig (*Cavia cobaya*) by Hensen, and the House-mouse, the Rat (*Mus decumanus*), and the Guinea-pig by Fraser. Slightly later, fresh light was thrown on the subject by Spee, and lastly Heape's researches on the Mole (*Talpa europea*) have supplied additional information.

The explanation of the phenomenon is briefly as follows. As has already been described, the solid mass of inner-layer cells, attached to one pole of the blastodermic vesicle in the Rabbit (fig. 39, *b, c*), flattens out to form the germinal disc (fig. 39, *d*).

In the Mole the primitive inversion of the blastoderm is retained slightly longer, the embryonic epiblast forming a cup-like depression at one pole of the blastodermic vesicle; the secondary cavity thus formed being filled with loose cells of epiblastic origin. The whole is roofed over by a layer of covering cells, which is continuous

with the outer wall of the blastodermic vesicle (compare fig. 45, n). Later, in Insectivore the blastoderm becomes flattened out, and development proceeds mainly as in the Rabbit.

In the Field-vole the ovum forms a normal blastodermic vesicle, with a blastoderm consisting of epiblast and primitive hypoblast (fig. 41). The layer of covering cells which overlies the embryonic epiblast is the seat of an early and rapid proliferation (fig. 83*, A), thus forming a mass of cells which pushes the blastoderm before (fig. 83*, B). The embryo is developed from the centre of the germinal area, the folds of the amnion arising between the embryo and the covering cells (fig. 83*, C).

In the House-mouse and Rat the blastoderm is pushed for a considerable distance within the blastodermic vesicle by the proliferating epiblast (fig. 83*, E). Subsequently an elongated cavity appears within the latter, extending along the whole length

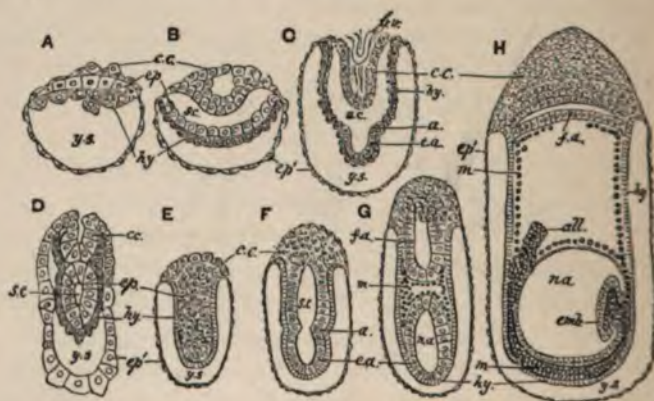


FIG. 83*.—DIAGRAMS ILLUSTRATING THE INVERSION OF THE GERMINAL LAYERS IN THE BLASTODERMIC VESICLE OF RODENTS.

A-C. Field-vole [after Kupffer]. D. House-mouse [after Selenka]. E-H. Rat [after Fraser]. None of the figures are drawn to scale.

a. commencement of the folds of the amnion; all. allantois; b.v. blood-vessel of uterine wall; c.c. covering cells which primitively overlie the blastoderm, and which serve to connect the future placental pole of the blastodermic vesicle with the wall of the uterus; e.a. embryonic area of blastoderm; emb. embryo; ep. embryonic epiblast; ep'. non-embryonic epiblast, or epiblast of blastodermic vesicle; f.a. false amnion or serous membrane; f.v. blood-vessel; h.y. hypoblast; m. mesoblast; n.a. neur-amniotic cavity (amniotic cavity); s.c. secondary cavity; y.s. cavity of yolk-sac or blastodermic vesicle. In the Rat (E-H) the wall of the blastodermic vesicle consists of two layers, epiblast and hypoblast; only the former is shown in the diagrams. The notch above the line pointing from m in H indicates the neur-teric canal, and marks the posterior end of the embryo.

the previously solid plug of epiblast cells. This cavity clearly corresponds to the hollow simple cup-like invagination of the blastoderm of the Mole and Field-vole. The germinal disc occupies the bottom of the depression, and the embryo develops on the upper surface of the secondary cavity (fig. 83*, H, emb); thus, to borrow an illustration, at a certain stage (fig. 83*, C, F) the embryo bears the same relation to the secondary cavity that the embryo Fowl does to the cavity of the amnion at an early stage in the formation of the amniotic folds (fig. 72, A, B). Whether it is rectified (Talpa) or not (Arvicola, Mus), the body of the embryo always lies morphologically outside the blastodermic vesicle.

The primitive elongated secondary cavity of the House-mouse and Rat soon becomes constricted into two vesicles, one of which occupies the fundus of the involution, while the other lies in its stalk (fig. 83*, F, G). The former has been named by Fraser the neur-amniotic cavity, as it is from the walls of this vesicle alone that the embryo is

formed. This vesicle is merely the isolated extremity of the primitive secondary cavity; its wall is composed of an inner layer of epiblast and an outer layer of primitive hypoblast, and the dorsal surface of the embryo consequently projects into its central cavity. In other words, it is the cavity of the amnion of more normal embryos (fig. 79, 3-5, *ah*).

The second vesicle encloses what Fraser terms the false amnion cavity. The epiblastic epithelium lining it is the exact equivalent of the false amnion or serous membrane of other Amniotes.

During further development these two vesicles become separated by a considerable space from one another. The mesoblast, which has by this time made its appearance in the embryonic area, extends into this "interamniotic space," and the allantois also penetrates into it as an, at first, solid bud of cells (fig. 83*, H, *all*). The interamniotic space into which the mesoblast and allantois immigrate is simply the extra-embryonic body-cavity (pleuro-peritoneal cavity) of other forms (figs. 72, 77, 78, *ca*).

The last term of the series is found in the Guinea-pig, in which Rodent neur-amniotic cavity, with its embryonic area, appears to be precociously separated from the upper pole of the blastodermic vesicle, so as to form a vesicle at the opposite pole. The neur-amniotic vesicle is thus a hollow ball composed of two layers of cells, the outer layer being the primitive hypoblast and the inner layer the epiblast. There is a thick ingrowth or plug ("Träger") of epiblast cells at the upper pole, as in the House-mouse (fig. 83*, D).

Summary of Evolution of Foetal Membranes.—Food-yolk is stored up in the primitive hypoblast of most Vertebrates, sometimes to an enormous extent. In the latter case the embryo is, as it were, pinched off from the large yolk-sac.

During its development the embryo digests and absorbs the yolk by means of the surrounding hypoblast and the vascular splanchnopleur. In the case of a few Elasmobranchs the vascular yolk also obtains nutriment directly from the blood-vessels of the enlarged oviduct (uterus) of the mother, prominences from the yolk-sac fitting into depressions of the oviduct. In the Teleost Anableps the vascular yolk-sac is provided with villi, which absorb nutriment from the fluid secreted by the walls of the dilated ovarian chamber, within which the embryos are developed [Wyman].

T. J. Parker finds in *Mustelus antarcticus* that the pregnant oviduct was subdivided into five to eight compartments, each containing one embryo. The wall of each compartment can be resolved into two layers: an outer highly vascular membrane (pseudo-chorion), derived from the oviduct; and an inner cuticular non-vascular layer, secreted by the former. As the enclosed cavity is tense with a fluid giving the reactions of the amniotic fluid, as generally understood, he proposes to call the latter membrane the pseudamnion.

In Birds, simple villi develop from the yolk-sac for the purpose of absorbing the albumen.

When the ancestors of the Metatheria (Didelphia) and Eutheria (Monodelphia) were ceasing to deposit their eggs, and were retain-

ing the by-this-time shell-less ova within the oviduct, the ova were placed in a most favourable condition for obtaining supplemental nutriment. The vascular yolk-sac would readily become slightly attached to the wall of the oviduct, as in some Elasmobranchs and Lizards (*Trachydosaurus* and *Cyclodus* [Haacke]).

The nutriment (blood of the oviduct or uterus, and probably the secretion of the uterine glands) thus at the disposal of the ovum was more easily assimilated than the yolk; and it is not surprising that the yolk-sac gradually lost its yolk, and that the embryo became entirely dependent upon the maternal blood-vessels. The yolkless yolk-sac of Mammals is known as the blastodermic vesicle.

The blastodermic vesicle was primitively the only means of connection between the embryo and the parent, as it still is in the Metatheria, and at first is in the embryos of the Eutheria.

By this time the allantois, from being an almost purely respiratory organ, became attached to the serous or subzonal membrane, and assumed a nutritive function. In Birds (and probably in Reptiles), the allantoic villi also absorb the albumen which lies within the egg-shell. In the Eutheria, the egg-shell being absent, the villi enter into direct union with the uterine wall. As the allantois became more closely attached to the uterus, it gradually usurped the functions of the yolk-sac, and eventually entirely superseded it.

The allantoic villi are collectively termed the placenta, and distinct lines of specialisation in the disposition of the villi and structure of the placenta can be traced in the Eutheria, the main object to be gained being the increase in the facility for transfusion between the maternal and foetal fluids. The result is that in the higher forms the villi become more complex, and instead of being readily withdrawn from the uterine crypts at birth, they fuse with the uterine wall, and thus form a deciduate, as opposed to a non-deciduate placenta.

The complex foetal membranes of the higher Eutheria are evidently the result of the gradual differentiation of pre-existing structures.

Amnion of Insects.—The Insects are characterised by possessing an embryonic protective membrane, which is termed the amnion. It consists of a reduplication of the epiblast, which extends over the ventral (neural) aspect of the body and encloses all the appendages.

The two amniotic folds unite and fuse in the median ventral line below the developing embryo, and the two membranes thus formed separate and constitute a double covering for the embryo, as in the case of the Amniota.

In the Insects, the two folds of the amnion are purely epiblastic in origin, but they may conveniently receive the same relative names as those of the Amniota, the outer one being called the serous membrane, and the membrane next to the embryo is termed the amnion proper.

If they have not previously disappeared, the amniotic membranes are either absorbed or cast off at hatching.

CHAPTER V.

ORGANS DERIVED FROM THE EPIBLAST.

As the epiblast constitutes the external skin of the embryo, it naturally has a protective function; and it gives rise in the adult to the epidermis, together with those portions of the organs of active or passive defence which arise from the epidermis. It further gives origin to numerous glands, and also to the nervous system and to the sensory portion of the sense-organs. The functions of this layer may be summed up as protective, secretory, respiratory, and sensory.

Protective Structures—Invertebrates.—When the outer skin (epidermis) of an animal consists of a single layer of cells, it is usually protected by a more or less continuous and structureless membrane or cuticle.

The cuticle may become cornified, as in most compound Hydrozoa and some Polyzoa; or calcified, as in the Hydrocorallinae and other Polyzoa; or chitinised, as in the majority of Arthropoda. In most Crustacea the cuticle is both calcified and chitinised. Such an indurated cuticle (exoskeleton) may be produced into spines and other weapons of attack or defence.

The horny axial skeleton (coenenchyma) of the Antipathidæ (and possibly of the Gorgoniidæ) has been shown by Von Koch to be the secretion of an invaginated ectodermal epithelium. It has been recently stated by Klaatsch that in some Hydrozoa (Clytia) the perisarc is produced by the outer layer of the ectoderm itself becoming chitinised. According to Von Koch and Fowler, the hard parts of the Hexacoralla are also probably secreted by the ectoderm. The cells which secrete the spicules of Alcyonaria are also of epiblastic origin.

In many cases the outer layer (ectosarc) of the protoplasm of the epiblast cells gives rise to one or numerous delicate contractile protoplasmic hair-like processes (flagella or cilia), which penetrate the cuticle, when present, and have a lashing movement. They serve for the progression of the embryo or adult, or to set up a

current in the surrounding medium for the procuring of food, aeration of the tissues, discharge of waste matter, and other purposes.

The epiblast cells (usually termed ectoderm) may in the Cœlenterata develop within themselves, by a modification of their own protoplasm, sacs containing a long coiled thread,—the thread-cells or nematocysts,—which can be suddenly projected and form powerful stinging organs. In the Turbellarian worms analogous short rods often occur.

The shells of Brachiopods are secreted by the outer surface of the delicate pallial membrane, and therefore may be regarded as a

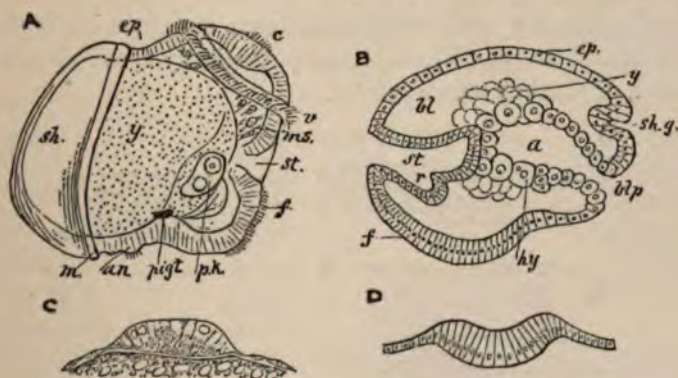


FIG. 84.—VELIGER LARVÆ OF MOLLUSCA.

A. Side view of veliger of Purple-snail (*Lanthina*). B. Longitudinal vertical optical section of early veliger of the Pond-snail (*Lymnaeus stagnalis*). [After Hoes.] C. Optical section of primitive kidney of embryo *Murex*. D. Section of shell-gland of the same.

a. archenteron; an. ciliated patch in position of future anus; bl. blastocœl (archicœl); blp. blastopore; c. tuft of cilia above thickened epiblast at the apex of the head; ep. epiblast; f. foot; hy. hypoblast; mn. mantle-fold; ms. mesoblast; pig. spot of violet pigment; p.k. primitive kidney; r. invagination to form the sac of the radula; sh. shell; sh.g. shell-gland; st. stomodæum; v. velum; y. yolk-cells, forming the liver in B.

special form of cuticle. The shells of adult Mollusca are composed of three layers, of which the cuticle or epiostracum ("epidermis") and the prismatic layer are secreted by the thickened edge of the mantle, while the general upper surface of the mantle secretes the nacreous layer.

In all Molluscan embryos an invagination of columnar epiblast (figs. 84 and 18) takes place on the dorsal side behind the velum. This is known as the shell-gland, and is of invariable occurrence: later it flattens out; the surface thus formed, the mantle, secretes the larval shell. In the Lamellibranchs the axial line of the shell-area remains uncalcified, and persists as the ligament and

hinge-line of the adult. The primitive shell of Mollusca at first forms the apex of the permanent one, but it usually disappears in time.

A pit-like depression of the mantle occurs in all embryo Cephalopoda, which may be termed the shell-sac. This soon atrophies in Octopus, while that of the Squid and Cuttlefish secretes the "pen" and "cuttle-bone" respectively. The shell-sac is often regarded as the equivalent of the shell-gland of other Mollusca, but Lancaster has shown that it cannot have the simple significance which it appears to possess: the student is referred to his paper for a statement of the argument. The conclusion arrived at is, in brief, that the shell-sac of embryo Cephalopoda is not only equivalent to the shell-gland of other Mollusca, but in addition corresponds with an upgrowth of mantle-folds over the original external shell, much in the same manner as the shell of *Aplysia* is concealed.

In all cases the shells of the Mollusca are entirely epiblastic in origin, and are consequently, morphologically speaking, always external, or exoskeletal, structures.

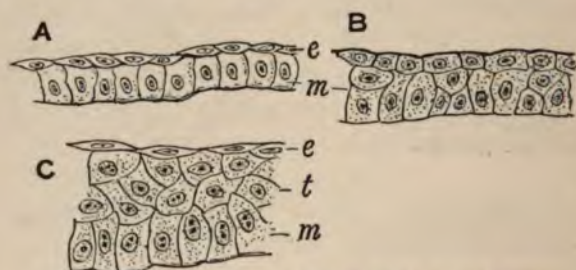


FIG. 85. SECTIONS OF SKIN OF EMBRYO BIRDS. [After Jeffries.]

A. Section of epidermis of 111 hours' Fowl embryo. B. Of 134 hours' Fowl.
C. Of 17 days' Duckling.

e. epitrichial layer; m. mucous layer; t. transitional cells.

Chordata.—In the majority of Chordata embryos the epiblast consists at first of a single layer (figs. 23, 26, 29–32, 43); but in the Anura (figs. 24 and 62) two layers are present. Of these two layers, the lower alone is the active layer, and from it are developed the glandular and nervous structures. In the Urodela the primitively single layer (figs. 58, 59) early becomes double, the lower one of which behaving as in the Anura.

The epidermis of *Amphioxus* permanently remains as a single layer.

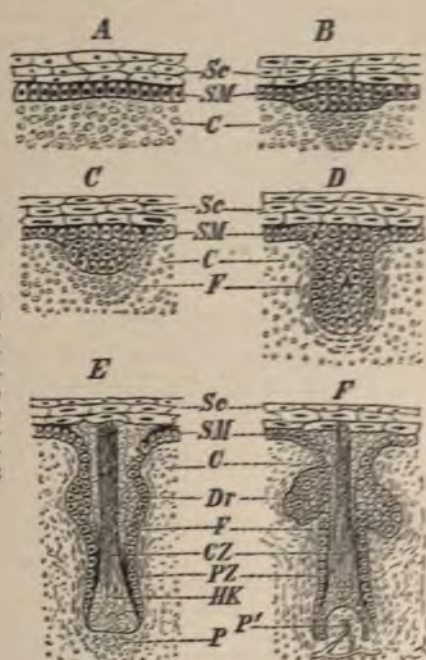
In all other embryo Vertebrates, the epiblast, from being single, becomes double layered, owing to the primitive epiblast giving rise to a layer of flattened epithelial cells, the epitrichial layer (fig. 85). This may be regarded as the primitive horny or protective layer of the epidermis. The lower layer is the mucous or Malpighian

epithelium, and persists throughout life as the active and regenerative layer of the epidermis. Later the mucous epithelium gives rise to cells of irregular shape which eventually become more or less spindle-shaped (transitional cells of Jeffries). The epitrichial layer is always shed, and the oldest transitional cells, by a process of drying and consequent shrinkage, become the horn-cells of the adult.

The horny layer is present in all the purely terrestrial Vertebrates (*e.g.*, Mammalia, Aves, and Reptilia), but not in other

FIG. 86.—SIX STAGES IN THE DEVELOPMENT OF HAIR.
[From Wiedersheim.]

C, derma; CZ, central zone of hair-germ, which forms the hair-shaft with its medulla or pith and its sheaths; Dr, sebaceous gland; F, mesoblastic sheath or follicle; HK, hair-knob; P, commencement of formation of hair-papilla; P', the same at a later stage when it has become vascular; PZ, peripheral zone of hair-germ, later giving rise to the outer root-sheath; Sc, stratum corneum of epidermis; SM, stratum Malpighii.



forms. In these latter there are parenchymatous cells very similar to an early stage in the development of the horn-cells.

The horn-cells are doubtless an adaptation to, or result of, an aerial life, and consequent drying of the surface of the body. Such protected surfaces as cavities of the ear and nostrils do not develop horn-cells, although the evanescent embryonic epitrichial layer is present. It is thus the effete epiblastic cells themselves which constitute the protective layer.

A transverse section of the epidermis of Man, which may be taken as being typical of Mammalia generally, shows a superficial horny layer (*stratum corneum*), and a deeper-seated Malpighian layer or *rete mucosum*. The latter has a basal layer of columnar cells, from which the whole epidermis is derived, and there is a complete transition between this layer and the flattened scales, which are thrown off the surface by desquamation. Anatomists usually distinguish several layers in the epider-

mis, but the three layers already referred to, the mucous epithelium, the transitional cells (= mucous layer), and the horny layer, are alone of morphological importance.

Nails, claws, hoofs, horny beaks, the horny sheaths of the horns of the Bovidæ, are merely local condensations of the horny layer of the epidermis, while hairs are similar linear extensions.

A hair commences as a minute solid ingrowth of the columnar layer of the epidermis into the derma (fig. 86). A small bulb, the hair papilla, containing nutritive capillaries, grows up from below

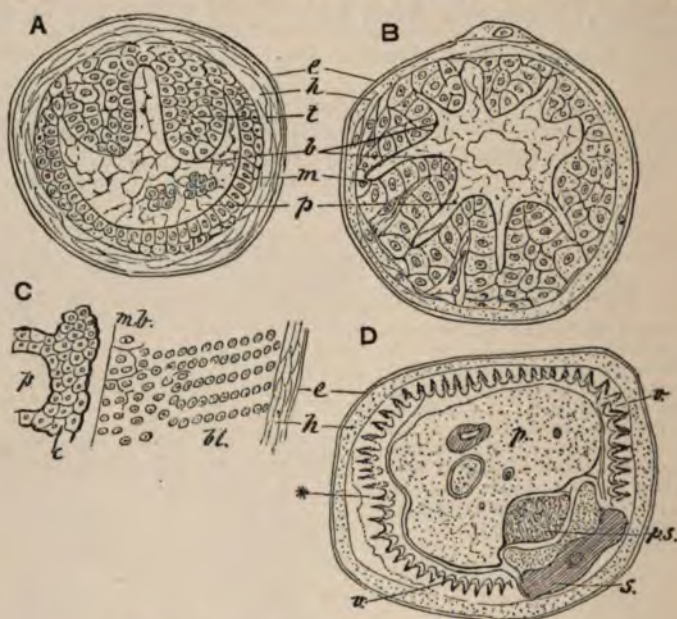


FIG. 87. DEVELOPMENT OF FEATHERS. [After Jeffries.]

A. Transverse section of a feather papilla near the tip, twenty days' Duckling. B. The same lower down of an eighteen days' Duckling. C. Longitudinal section of the same as A; there is a capillary within the pulp full of blood-corpuscles. D. Transverse section of a pin-feather of an embryo Robin.

b. primitive barbs; bl. incipient barbules; c. capillary; e. epitrachial layer; h. horn cells; m. mucous or Malpighian layer; m.b. mucous layer of barb; p. pulp; p.s. pith of shaft; s. shaft; t. transitional cells; v. vane; * point of division between the two vanes.

into the hair follicle. The outer cells of this papilla elongate, become cornified, and thus form a hair, which soon forces its way to the exterior through the follicle.

Down-feathers arise from large papillæ, which contain a central vascular mesoblastic pulp; as the papillæ grow in length, they tend to sink below the surface, more especially at the posterior side, thus producing the backward slant of most feathers; the depressions are known as feather-follicles. Two thickenings of the epidermis appear on the upper surface of the papilla and encroach on the pulp, starting from the top, and slowly extending downwards (fig. 87, A, b). Whilst these first

two barbs are growing, the epitrichial layer becomes more compact and the transitional cells horny, thus forming a protective case for the incipient feather. As the papilla grows, more barb folds appear (fig. 87, b, b). The barbs are formed by the cells at the angle of the thickenings, as seen in section, while the cells on the sides arrange themselves in columns (fig. 87, c, c), which bend slightly towards the tip of the papilla, and ultimately form the barbules. The walls of the cells of the barbs and barbules finally become converted into a kind of horn, and the protoplasmic contents dry up.

The contour feathers of adult Birds are developed upon the same plan as the down-feathers, by a renewed growth of the primitive papilla. Two primary barb-folds appear as before, and are very shortly followed by numerous others. The two primaries unite to form the two halves of the shaft, and are joined later by those on the sides. At the side of the papilla, opposite to that where the shaft is formed, is a slight inversion of the mucous epithelium; it is here that the separation will occur which results in the two vanes of the feather. As the barbs are set at an angle of about forty-five degrees, the portions farthest from the shaft in a transverse section are sections of the tips of lower barbs. In feathers with a hollow shaft, the two sides bend in and enclose a column of the pulp (fig. 87, d), which subsequently dries up; in solid shafted feathers the sides are simply flattened together. When the feather is matured, the covering falls off and the pulp withers away, and the barbs separate into the two vanes. Thus it comes about that the upper surface of the shaft and barbs of a feather (together with the whole of the barbules) is formed from horn cells or modified transitional cells, whereas the lower surface is composed of degraded mucous epithelium. The quill is produced by a cornification of the walls of the lower portion of the papilla.

As hairs consist of the horny layer of the epidermis only, it is evident that they can scarcely be regarded as strictly homologous with feathers; the latter are never found out of the group of Birds, and the former are equally peculiar to Mammals.

The scutæ which occur on the legs of Birds are mere folds of skin with a horny layer, a mucous epithelium, and a mesodermal core. They occasionally bear feathers.

The scales of Snakes, of *Chelonia* (tortoise-shell), and also of some Lizards are purely epidermal structures; but those of other Lizards (*Anguis*, *Cyclodus*, *Scincus*) and the scutes of Crocodiles, and of the Armadillos amongst Mammals, are partly derived from the epidermis, but chiefly from the corium; in other words, they are mainly of mesoblastic origin (see p. 193). The scales of the *Manis*, like the horn of the *Rhinoceros*, are formed of hairs agglutinated together.

Teeth are not purely epiblastic organs, but they may be conveniently dealt with here. There is little doubt that teeth were primitively structures similar to the placoid scales of Elasmobranchs which have been retained and emphasised in the jaws.

A placoid scale arises as an ingrowth from the derma into the epidermis, the basal columnar cells of the latter are pushed up and

thus form a kind of sheath to the papilla. The basement membrane which is a product of the epidermis, becomes thickened and calcified at the apex of the papilla, and constitutes an enamel cap, the papilla becoming converted into dentine, bone, and pulp. The point of the scale eventually forces its way to the exterior.

In the development of a milk (deciduous) tooth a prolongation from the epidermis arises which passes into the derma (fig. 88) the inferior end becomes dome-shaped, forming the "enamel organ" (fig. 89). A papilla of the derma projects into the hollow of the dome, and soon becomes vascular; the papilla produces the dentine and cement of the tooth, while the columnar layer of the

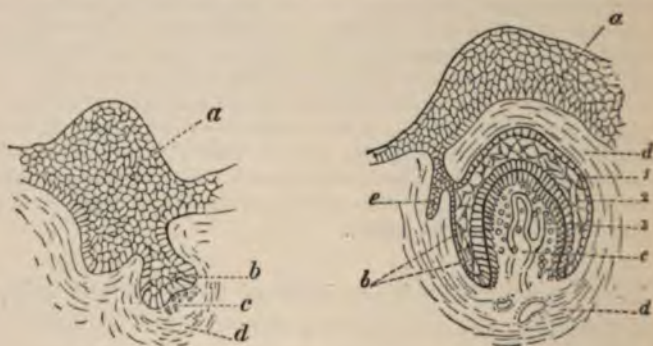


FIG. 88.

FIG. 89.

EARLY STAGES IN THE DEVELOPMENT OF MILK-TEETH.

[From Landois and Stirling.]

FIG. 88.—*a*, dental ridge; *b*, commencement of the enamel organ; *c*, dentine germ, first trace of the pulp; *d*, first indication of the mesoblastic investment or tooth-sac.

FIG. 89.—*a*, dental ridge; 1 upper, 2 lower or secreting layer of the enamel organ (*b*); 3 intermediate epiblast cells; *c*, dental papilla, with capillary; *d*, commencement of dental sac; *e*, enamel germ of the corresponding permanent tooth.

enamel-organ or germ, which overlies the papilla, is stated to secrete the enamel layer (fig. 90). The permanent teeth are similarly developed, but the enamel germ arises as a bud (fig. 89, *e*) from that of the deciduous tooth. Huxley, and after him Miss Nunn, asserts that the enamel, like the dentine of teeth and scales, owes its origin to odontoblasts, and is therefore mesoblastic; and that the cuticula dentis is formed by the metamorphosis, either in whole or in part, of the enamel cells, which have nothing whatever to do directly with the formation of the enamel. However this may be, the large size and the invariable presence of the enamel organ prove that it has, or has had, an important function in the production of teeth.

In Elasmobranchs all the teeth of each jaw are developed from a common rod of tissue, which is derived from a ridge-like proliferation of the mesoblast into the epidermis of its jaw. The enamel cap of each tooth is formed in the same manner as in the placoid scales.

Scott finds that the horny teeth of the metamorphosing Lamprey are developed from the deeper layer of the epiblast which rises in a cap-like manner over a mesoblastic papilla: this appears to be the representative of the enamel organ. A second tooth is developed vertically below the first. The original papilla and enamel organ are functional throughout the life of the animal.

Horny teeth and a horny sheath to the jaws occur in larval Anura.

Epiblastic Glands.—The epidermis is the seat of origin of many and varied glands. The simplest cases are where certain cells become enlarged and secretive, forming unicellular glands. These



FIG. 90.—LATER STAGE IN THE DEVELOPMENT OF A TOOTH. [From Wiedersheim.]

Bg. connective tissue which forms the dental sac; *D.S.* dentine; *E.M.* epithelium of mouth; *Ma.* membrana adamantina (cuticula dentis); *O.* odontoblasts; *SK.* enamel germ; *ZK.* tooth germ.

alone occur in the Cœlenterata; in higher forms they often co-exist with multicellular glands.

Multicellular glands may be simple (figs. 18, 84) or compound (figs. 91, C-E; 93, A, *m.gl.*; 141, F). The development of such a very complex gland as a salivary or mammary gland is as follows:—A simple solid process from the epidermis sinks into the derma; branches sprout out from its blind end; these acquire a central cavity, elongate, and greatly increase in number, until a much-branching tubular organ is developed. The ultimate ramifications in the above-mentioned glands expand into secretory pouches or alveoli.

Although there is a solid ingrowth of the epidermis, it is the Malpighian layer alone which forms the secretory tissue of the gland; the central epidermal cells eventually disappear. The solid ingrowth of the incipient gland is clearly a secondary process.

Other glands may always remain simple tubes, or at most become slightly branched.

Thus the most complex type of gland reproduces in its own development those simpler conditions which it must have passed through in the course of its evolution, and which are severally the permanent states of other glands. In the simplest glands all the cells are secretory, but as complication arises the stem and main

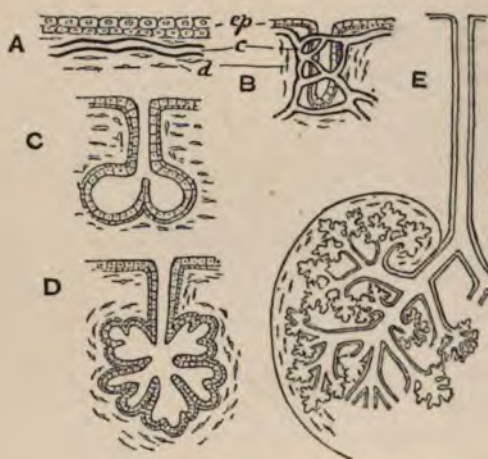


FIG. 91.—DIAGRAMS TO ILLUSTRATE THE EVOLUTION OF COMPLEX GLANDS. [After Huxley.]

A. Section of an ideally simple skin, showing the mucous and horny layer of the epidermis (*cp*), and a capillary (*c*) within the derma or cutis (*d*). B. A simple gland, with its capillary network. C, D, E. Glands of increased complexity. The vascular supply is omitted in these figures.

branches lose this function and constitute ducts to convey the fluid secreted by the terminal portions.

All the glands opening on the general surface of the body are of epiblastic origin; such are the sweat, scent, anal, poison, adhesive, byssus, slime, spinning and mammary glands. The salivary glands of Insects develop as paired invaginations from the ventral plate of the mouth, behind the stomodæum, and on the inner side of the mandibles.

According to Klaatsch, the mammary glands develop from a shallow depression, the glandular area or areolar epithelium, the margin of which is slightly raised. This condition is permanent in Monotremes (fig. 92). In adult Man, the glandular area is raised to form the nipple; the same occurs in the Mouse, but the glands have a single duct. The nipple of Carnivores, Pigs, Horses, and especially that of Ruminants, is formed by the upward growth of the raised margin in such a manner that the glandular area forms a pit, at the bottom of which the glands open.

It seems probable that the mammary glands are greatly enlarged and modified sebaceous glands, the hairs to which they belong having disappeared in course of

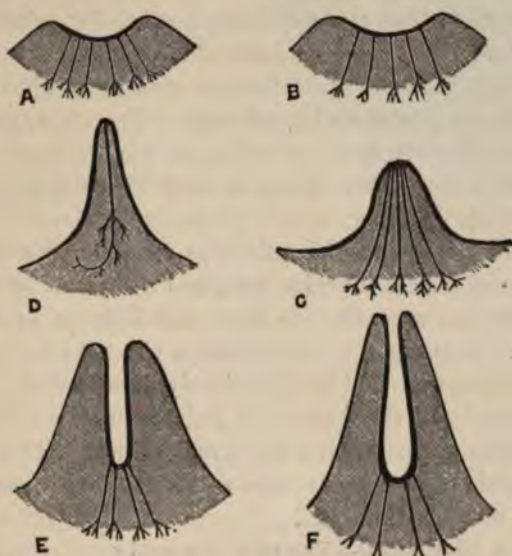


FIG. 92.—DIAGRAMS OF THE ARRANGEMENTS OF THE DUCTS OF THE MAMMARY GLANDS IN VARIOUS MAMMALS. [From Bell after Klaatsch.]

The glandular area of the epidermis is indicated by the thicker line.

A. Adult Echidna. B. Human embryo. C. Human adult. D. Adult Mouse. E. Embryo Cow. F. Adult Cow.

time (see figs. 86, E and F, *Dr*; 93, B, *h*); but Rein denies this, and believes that they are organs *sui generis*. Gegenbaur has lately shown that the so-called mammary

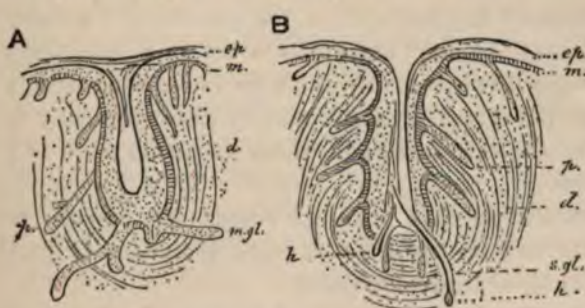


FIG. 93.—DEVELOPMENT OF MAMMARY GLANDS OF MARSUPIALS.

A. Embryo of *Phalangista vulpina* (0.5 cm.) B. The same of *Perameles gunii* (8.6 cm.) Vertical section through rudiment of the mammary depression. [After Klaatsch.]

d. derma; ep. horny layer of epidermis; h. hair; m. Malpighian layer of epidermis; m.gl. milk-glands; p. processes of Malpighian layer, indistinguishable from hair or gland rudiments; s.gl. sebaceous gland.

glands of the Monotremes are phylogenetically distinct from those of other Mammals. They consist of tubular glands, modified derivatives of the sudoriferous type.

Those glands derived from the stomodæum (p. 110) and proctodæum are also epiblastic in origin.

In the "Veliger" larval stage of marine Prosobranch Gasteropoda a group of epiblast cells, on each side of the body behind the velum enlarge, become vacuolate, and constitute what are generally regarded as provisional renal organs (fig. 84, A, *p.k.*, c). The red or violet pigment spots occurring in the Veligers of Opisthobranchs and a few other Molluscs may be of a similar nature (fig. 84, A, *pgt.*).

De Meuron describes the primitive renal organs of *Helix* as arising from epiblastic invaginations, and not as being mesoblastic in origin, as are, according to Rabl, the kidneys of the aquatic Pulmonata. This organ is a tube with a ciliated internal orifice as in other Pulmonata. Fol had previously described the provisional excretory organs of the terrestrial Pulmonates as a pair of non-ciliated epiblastic pits, with no internal orifice. The permanent kidney appears to be formed as an epiblastic invagination supplemented by mesoblastic tissue.

Muscular Elements.—The root-like prolongations of the large ectodermal cells of Coelenterates are contractile, and practically form an external muscular sheath to the body. The brothers Hertwig have demonstrated distinct ectodermal muscle-cells in the Actiniæ, and Hubrecht has found similar cells in the Nemertea.

The non-striated muscle-fibres which surround some sweat glands are stated by Ranvier to be derived from the epidermis in Man.

Respiratory Organs.—From the nature of the case, the external skin of the body must always act as a respiratory surface, except when it is surrounded with an impervious cuticle or exoskeleton; but certain areas are usually more especially devoted to the interchange of those gases which constitute what is known as respiration.

Invertebrates.—The external organs for aquatic respiration are mostly delicate filaments or plates (branchiæ or gills), within which the blood freely circulates.

The manner in which such organs are developed is so self-evident as to need no special comment. In certain cases, as, for example, in the gills of some Lamellibranchs (*e.g.*, *Anodonta*, *Dreissena*), the primitively simple bent gill-filaments form the perforated plate-like gills of the adult by concrescence between their two limbs, and by the union of the filaments with each other.

It may be here noted that the respiratory plumes of Serpulaceæ

amongst the Chaetopoda are supported by (probably mesoblastic) cartilaginous bars.

Hartog and others have shown that anal respiration occurs in probably all larval Crustacea, and also in some adults. Leaf-like respiratory organs occur in the rectum of larval Dragon-flies. It will be shown that in the Arthropoda the rectum is derived from the proctodæum (see p. 111).

Aerial respiration has supplemented branchial respiration in some Mollusca and Crustacea by the upper portion of the branchial chamber becoming vascular and functioning as a lung (*e.g.*, Ampullaria, Birgus). In the Pulmonate Mollusca the gills have entirely disappeared. Lankester has suggested the probable evolution of the pulmonary sacs of the aerobranchiate Arachnida (Scorpions and Spiders) from the lamellate gills of their Limulus-like ancestors (Hæmatobranchiata).

The tracheæ of the tracheate Arthropoda appear to have been derived from simple diffused cutaneous glands, which have evolved into delicate branching respiratory tubes.

Hubrecht has shown that the ciliated pits which penetrate the posterior brain-lobes of the higher Nemertean worms arise solely from the epiblast, and not partially from the œsophagus, as previous observers had stated. It is probable that these pits have a sensory as well as a respiratory function.

Chordata.—The epidermis is undoubtedly respiratory in some Chordata, especially amongst the Amphibia.

The characteristic respiratory organs of the Chordata are of hypoblastic origin (see p. 177).

External or epiblastic gills are, however, developed in a few forms. These are the larval external gills of the Ganoid Polypterus, the Teleost Cobitis, and the permanent external gills of the Dipnoid Protopterus, and of some Urodeles. In other Amphibia they are purely larval organs. The so-called external gills of embryo Elasmobranchs are merely the extremely long filaments of the internal gills of the posterior lamellæ, only, of each arch, which protrude beyond the clefts.

In certain Teleosts (*e.g.*, Anabas, some Siluroids) accessory respiratory organs, which are supported by very delicate contorted bony plates, may grow out from the upper portion of the gill-arches into the branchial chamber (p. 179). They are thus necessarily invested by the epidermis, and constitute organs for aerial respiration. In Saccobranchus and a few other Fishes, air is respired by means of membranous sacs which evaginate from the branchial chamber and push their way along the lateral muscles of the body. These Teleosts have thus acquired new epiblastic organs for breathing air direct; but the problem of aerial respiration has been more satisfactorily solved by the utilisation of the air-bladder of Fishes and the development of lungs in the ancestral Amniota.

Stomodæum.—The invagination of the epiblast, which in most animals forms the mouth of the adult, is known as the stomodæum. There is reason to believe, as has already been stated (p. 75), that in the Invertebrates the stomodæum corresponds with the anterior extremity of the primitive mouth (blastopore). In the Chordata the same interpretation is held by some embryologists, but Dohrn and his school believe that the stomodæum is a new formation possibly corresponding to a pair of fused gill-slits.

Whatever theory may be held concerning its nature, the fact remains that in a large number of animals the mouth arises as an epiblastic invagination which subsequently unites with the blind anterior end of the mesenteron (archenteron). The following types will serve as examples:—*Asterias* (fig. 52), *Lymnæus* (fig. 84, B), *Astacus* (fig. 140), and *Petromyzon* and *Bombinator* (fig. 94).

Usually the stomodæum forms but an insignificant portion of the alimentary canal; but in the Arthropoda, especially in the Crustacea (fig. 140, *f.g.*), it is of considerable size. In the latter group the stomodæum forms the large crop or masticatory "stomach," which in the Decapoda is complicated by the development of the gastric mill and the filtering apparatus. In Insects it forms the œsophagus, crop, and proventriculus or gizzard, when such are present. The mouth, œsophagus, and masticatory apparatus of Rotifers are also derived from the stomodæum.

All the structures and glands developed from the stomodæal epithelium are necessarily of epiblastic origin, amongst which may be mentioned the radula sac of Mollusca (fig. 84 B, *r*), with its contained odontophore, the enamel organ of teeth, and various mucous and salivary glands, but not the salivary glands of Insects.

The Pituitary Body (Hypophysis Cerebri).—The pituitary body arises in most Vertebrates as a tubular invagination of the roof of the mouth (stomodæum) approaching the infundibulum (see p. 127). The upper end becomes swollen, and the stem gradually atrophies. The enlarged distal portion, which is surrounded by vascular tissue, becomes lobed, and the central lumen may or may not persist; it ultimately enters into close union with the infundibulum (figs. 107, *hph*; 108, *pit*, 109, H; 112, *hp*; 116, *hph*); but it is only in the Mammalia that the two structures fuse with one another.

According to Scott, the pituitary body arises in the Lamprey as an epiblastic invagination between the olfactory epithelium and the stomodæum (fig. 94, A). In the Frog it appears before the invagination of the stomodæum; but owing to the large

size of the latter, and the rapid growth of the cerebral hemispheres, the pituitary body is carried into the mouth (fig. 94, c). In other forms the early development of the cerebral lobes, probably combined with a later appearance of this now functionless organ, causes it to be apparently derived from the roof of the stomodæum itself.

Miss Johnson and Miss Sheldon state that in the Frog and Newt the stomodæum is at first a solid ingrowth of the deeper layer of the epiblast; the lower part of the ingrowth fuses with the fore-gut, while the upper part projects freely and forms the pituitary body.

In Teleosts, according to Dohrn, the hypophysis arises as a pair of hypoblastic evaginations in front of the mouth, and Hoffmann finds that the earliest rudiment of the hypophysis is developed in the common Snake from the anterior end of the archenteron; the same apparently occurs in the human embryo (fig. 143, *R.p.*).

The organ has probably a pre-vertebrate, and possibly a pre-chordate, significance.

Proctodæum.—The arguments in favour of the stomodæum corresponding to the anterior end of the primitive blastopore of

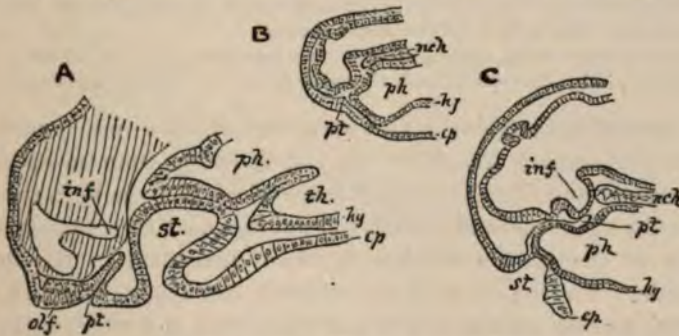


FIG. 94.—DIAGRAMS TO ILLUSTRATE THE RELATION OF THE PITUITARY INVAGINATION TO THE STOMODÆUM.

A. Longitudinal vertical section through the head of an embryo Lamprey just before hatching [from Scott]. B, C. Similar sections through the head of an embryo, and of a young Tadpole, respectively, of a Toad (*Bombinator*) [from Scott, after Götte].

ep. epiblast; hy. hypoblast; inf. infundibulum; nch. notochord; olf. olfactory epithelium; ph. pharynx; pt. pituitary invagination; st. stomodæum; th. thyroid invagination.

Invertebrates apply to the proctodæum with regard to its posterior extremity. The blastopore, or a portion of it, however, often persists as the anus, or the anus shortly appears at the spot where it has closed up.

Any invagination of epiblast at the anus constitutes a proctodæum. In most Invertebrates the proctodæum is small, but the long rectum of Crustacea (fig. 140) is derived from this invagination; it is also large in other Arthropods.

The Malpighian tubules of the Arachnida and Insecta arise as a single pair of evaginations from the anterior portion of the proctodæum; but these usually increase in number.

The proctodæum forms the cloaca of many of the lower Verte-

brates, or at all events its outer portion, the anterior section being formed by the dilated end of the alimentary canal, into which the urogenital organs open (figs. 73, 143, c). The epiblastic section of the cloaca is sometimes marked off from the hypoblastic portion by a small fold.

Cloaca of Amniota.—In a recent paper Gadow states that “the cloaca of the Amniota consists originally, either permanently or in the embryo only, of three successive chambers. I. The *Proctodæum* [Lankester]. The outermost anal chamber of epiblastic origin, with its derivatives: (1.) bursa Fabricii in Birds, (2.) various hedonic glands in most Amniota, (3.) the copulatory organs, the, at least partly, epiblastic nature of which is indicated by the frequently developed horny armament of the glans, by the various sebaceous glands, and by development. II. The *Urodæum* [Gadow]. Hypoblastic, this is the middle chamber or primitive cloaca, into which open the urinogenital ducts and through which pass the fæces. With its differentiations: (1.) urinary bladder, ventral; (2.) anal sacs in Tortoises, dorsal. III. The *Coprodæum*. This is the innermost cloacal chamber.

“The urodæum is the oldest portion of the whole cloaca, then follows the proctodæum, and, lastly, the coprodæum has secondarily assumed cloacal functions.”

Nervous System.—The nervous system and the sensory surfaces of the sense-organs are, as has been stated, derived from the epiblast. In scarcely any other section of Embryology is more light thrown upon the significance of the facts of development by a comparative study of the adult condition of these structures in the lower animals. For the sake of convenience the development of the central nervous system will be first considered, and afterwards that of the sense-organs.

Invertebrates.—In the majority of Invertebrates the central nervous system originates from certain areas of the epiblast. The cells of these areas are usually more or less columnar, and undergo rapid cell-division (proliferation). The mass of cells thus formed sinks into the underlying mesoblast, and eventually differentiates into nerve-cells or ganglion-cells, and into nerve-fibres. Outgrowths from the incipient nerve-centres (ganglia) form nerves and commissures.

Nerve-cells and nerve-fibres occur in all the higher or more active Coelenterata. They are undoubtedly modified ectodermal cells which have assumed a deeper position, and in the case of nerve-fibres have become greatly elongated. As all the ectodermal cells are connected with one another by means of their basal root-like processes, the nervous system is from the first connected with the superficial ectoderm cells on the one hand, and the deeper seated muscle-cells on the other, that is, of course, when the latter are present.

This undifferentiated nervous system is generally diffused over certain areas, chiefly the oral surface, or it may be restricted to a circum-oral ring, as in certain Hydroids.

Even in adult Starfish the nervous system is scarcely separated from the epidermis; and it has recently been shown that in most Echinoderms a nervous network surrounds the whole animal. There is, however, a more concentrated nervous tract round the mouth and along the ambulacral areas in all Echinoderms. The Carpenters and Marshall have proved the existence of an additional aboral nervous system in Crinoids.

A diffused nervous system lying immediately below the epidermis occurs, according to Hubrecht, in the lower Nemertean worms, in addition to the lateral cords of the higher forms (see also p. 165).

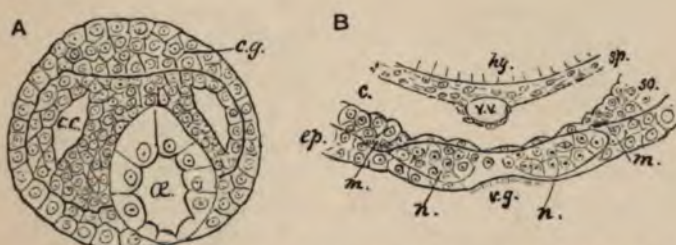


FIG. 95.—SECTIONS TO ILLUSTRATE THE DEVELOPMENT OF THE NERVOUS SYSTEM IN AN EARTHWORM (*Lumbricus trapezoides*). [After Kleinenberg.]

A. Through the head. c.g. cephalic portion of the body-cavity; c.g. cephalic ganglion; a. oesophagus.

B. Through the ventral wall of the trunk. c. body-cavity; ep. epiblast; hy. hypoblast; m. longitudinal muscles; n. ventral nerve cord; so. somatic mesoblast; sp. splanchnic mesoblast; v.g. ventral groove; v.v. ventral blood-vessel.

Hatschek describes the nervous system of *Criodrilus* as first arising as an anterior ectodermal thickening which extends backwards as a cord on either side of the mouth forming the oesophageal commissures. The process of thickening continually extends backwards, resulting in the formation of the double ventral nerve-cord. The nervous system of the Earthworm (*Lumbricus*), according to Kleinenberg, develops from the epiblast as two long cords on each side of a shallow ciliated median ventral groove (fig. 95). The two cords early unite, and segmental ganglionic enlargements are soon indicated. The cephalic ganglion is apparently at first quite independent of the ventral cords. Hatschek states that the ventral groove invaginates, and takes part in the formation of the nerve-cord.

In the Mollusca the nervous system is usually developed in the

ordinary manner by proliferation of the epiblast. This occurs in two regions. In the early Veliger larva of Gasteropods, or at the corresponding stage of other Molluscs, a pair of cephalic plates is formed on the pre-oral lobe within the velum by the rapid cell-division of the locally thickened epiblast. These give rise to the cephalic ganglia. The pedal ganglia arise from a pair of similar areas in the foot. Fig. 96, A, shows the proliferating areas which are giving rise to the cephalic and pedal ganglia in a Prosobranch Gasteropod (*Purpura*); these are seen in section in fig. 96, B.

The nerve-cords of Chitons have been shown by Kowalevsky to arise throughout their whole length from the epiblast in the region corresponding to that which they occupy in the adult. They form, in fact, a double nervous ring surrounding the latero-ventral aspect of the body. On recalling the relationships of the mouth and anus with the primitive blastopore (p. 76), it will be found that the nervous system

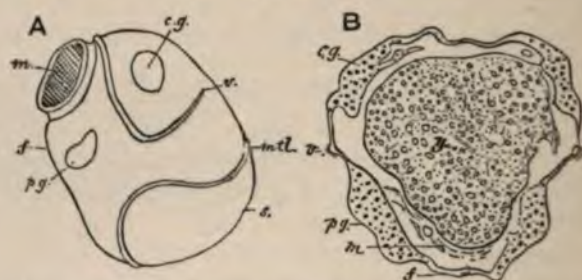


FIG. 96.—ORIGIN OF NERVOUS SYSTEM IN THE DOG-WHEELK (*Purpura*).

A. Side view of early veliger. B. Transverse section of the same.
c.g. cephalic ganglion; f. foot; m. mesoblast; mtl. mantle edge; p.g. pedal ganglion; s. shell; v. velum; y. yolk.

of these primitive Mollusca constitutes a double circum-oral ring, in other words, a nervous system comparable with that of many Coelenterates.

Kowalevsky also finds that in *Dentalium* the cephalic ganglia are derived from pit-like invaginations of the cephalic plates. The depressions soon lose their connection with the external epiblast and later their central cavity disappears. The pedal ganglia at first arise from an unpaired area; this divides, and each ganglion increases at the expense of the epiblast of the foot.

Lankester states that in the Cephalopoda, the white body originates from the epiblast of the head in the same manner and in the same position as the cephalic ganglia in other Mollusca, but that the true ganglia are of mesoblastic origin, the white body becoming an apparently functionless structure.

Bobretzky also derives the nerve-ganglia of Cephalopoda and of the Prosobranch Gasteropod *Fusus* from the mesoblast. Two explanations suggest themselves. 1. That the earliest stage of these structures has not yet been observed. 2. That if the observations are correct, it is a secondary phenomenon due to precocious segregation (see p. 165).

The formation of the nervous system in the Lamellibranchiata is, so far as is known, quite normal.

The ventral nerve-cord in the Crayfish arises in the median ventral line on each side of a central groove; this thickened epiblast is continued along anteriorly round the stomodæum, and passes into the incipient cerebral ganglia, which are formed in the centre of the pro-cephalic lobes.

According to Reichenbach, the development of the nervous system is somewhat more complicated, but the above account is probably substantially correct.

The development of the nervous system is very uniform throughout the Arthropoda; the ventral cord may arise as a single or a double thickening of the ventral epiblast; the median groove may be shallow, deep, or absent: it is stated to sometimes take part in the formation of the nerve-cord. The cerebral ganglia are apparently always continuous with the ventral cord.

The series of ganglia and the commissures connecting them, which together constitute the central nervous system of Invertebrates, is thus developed directly from the epiblast. These commissures are usually composed of nerve-cells as well as of nerve-fibres; in fact, the ganglia are merely local thickenings of the commissures with a preponderance of the nerve-cells.

The nerves proper develop as prolongations from the central nervous system, and may give rise to other ganglionic enlargements.

Nature of the Invertebrate Brain.—The portion of the central nervous system situated in front of the mouth (pre-oral) is always associated with the eyes, and constitutes the primitive brain. Lankester has appropriately termed this the archi-cerebrum. All the nerves which originate from it supply the pre-oral region of the head.

The brain of most, if not of all, Worms is an archi-cerebrum, as is also the pre-oral nervous system of the Amphineurous Mollusca (*Neomenia*, *Chiton*).

There is a tendency in the Arthropoda for the anterior appendages with their ganglia to shift forwards. In this manner a composite brain (syn-cerebrum) is formed. As the nervous system is composed of two lateral halves, there is no antecedent improbability in the migration forward of the ganglia.

All the appendages of the Nauplius larva of Crustacea are post-oral; and Pelseneer has recently shown that in *Apus* the ganglia of the first pair of antennæ have migrated to the brain, although their nerves apparently arise from the œsophageal commissure. The concentration is still greater in other Crustacea; thus in this group the brain is always a syn-cerebrum.

Balfour has shown that in the Spider the ganglia of the Chelicæ are post-oral, but they soon become fused with the pre-oral ganglia.

The antennæ of Insects and Myriapods develop from the pro-cephalic lobes, and are always innervated by the pre-oral ganglia. Therefore the antennæ of these forms

are probably not homologous with those of the Crustacea, and their brain is an archicerebrum. Hatschek states that the ganglia of the mandibular segment disappears in the œsophageal commissures, and that the sub-œsophageal ganglion is formed by the ganglia of the two maxillary segments.

An analogous concentration occurs in the brain of the higher Mollusca.

There is in the embryos of Arthropoda a pair of ganglia for each segment of the body, but a fusion of ganglia often occurs in the thoracic region of the body, notably in the case of the Brachyura and Spiders; in the former case the concentration occurs around the sternal artery.

Central Nervous System of the Chordata.—Throughout the Chordata the central nervous system appears very early, usually as a more or less well-defined plate of columnar epiblast (neural or medullary plate) in the median dorsal line of the embryo (figs. 59, 61, 97, 100). A central shallow longitudinal groove (neural or medullary groove) appears in this plate; it is often widely open at both ends. The neural plate extends from the dorsal rim of the blastopore to what will be the anterior extremity of the embryo.



FIG. 97.—EMBRYO OF FROG, WITH SPLIT-LIKE BLASTOPORE AND WELL-DEVELOPED NEURAL FOLDS. [After O. Hertwig.]
bl. blastopore; d.f. dorsal furrow; n. neural folds.

The walls of the neural groove bend over, and, fusing in the median line, convert the groove into a canal, the neural or medullary canal (figs. 63, 64, 102). The enlarged anterior portion of the neural tube is the incipient brain; the remainder will develop into the spinal cord. Before closing over the canal becomes ciliated in Amphioxus and the Fowl.

Neurenteric Canal.—In those Vertebrate embryos which have but little food-yolk, the blastopore occurs as an opening from the archenteron to the exterior, and the neural groove arises immediately dorsal and anterior to it; the neural folds, as a matter of fact, extend round each side of the blastopore (fig. 97).

The supposed relation of the blastopore of such embryos to the primitive blastopore, and the position of the latter with regard to the nervous system, has already been briefly mentioned (p. 76).

When the neural folds unite in the median line to form the neural canal, their posterior portion which surrounds the blastopore may also close over. By this means the blastopore would be shut off from the exterior by this overgrowth, and would necessarily open into the posterior extremity of the neural canal. The short

tube connecting the cavities of the nervous system and archenteron is known as the neurenteric canal (fig. 99, *ne*). The ventral portion of the canal is also termed the post-anal gut.

It was till quite recently supposed that this occurred in the Cyclostomi and Amphibia; but in these groups it appears that the blastopore persists as the anus, consequently what was termed the post-anal gut (solid in the Newt), which was imagined to extend between the closed-over blastopore and the new anus, is merely a ventral extension of the neural canal, owing to the growth of the tail taking place above the blastopore (figs. 98, 99).

FIG. 98.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE EMBRYO OF A FROG. [From Balfour after Göttsche.]

al, alimentary canal (archenteron); *m*, mesoblast; *nc*, neural canal; *yk*, yolk-cells; *x*, point of junction of epiblast and hypoblast at the dorsal lip of the blastopore. For the sake of simplicity the epiblast is represented as if composed of a single row instead of two layers of cells.



In those forms in which the blastopore, as such, is obsolete, being partially represented by the primitive streak (see p. 41), the neurenteric canal may be lost, but in many (*e.g.*, Lizard, Goose, Duck, Parrot, Mole) it still occurs and occupies the same relative position. In the Fowl and other Amniota the canal is lost, but traces of it may occur.

The closure of the neural groove takes place from behind forwards in Tunicates and Amphioxus, but usually in Vertebrates it

FIG. 99.—LONGITUDINAL SECTION THROUGH AN ADVANCED EMBRYO OF A TOAD (Bombinator). [From Balfour after Göttsche.]

an, anus, this should be represented as an opening into the alimentary canal; *ch*, notochord; *l*, liver; *m*, mouth (stomodaeum); *mc*, neural (medullary) canal; *ne*, neurenteric canal,—between this and *an* is the so-called post-anal gut; *pn*, pineal gland.



first closes in the region of the neck or hind-brain (fig. 100). The closure in some cases takes place more rapidly backwards, but in others the brain is the first to close over (fig. 101).

It is important to note that in the Tunicates and Amphioxus an anterior pore (neural pore) persists for some time after the rest of the canal is completed. At this stage (fig. 57, *oe*) the cavity of the archenteron can only communicate with the exterior through this pore. For suggestions concerning a possible significance of this arrangement, the reader is referred to papers by Sedgwick and Van Wijhe.

In the Teleostei, Lepidosteus, and Lamprey (fig. 61, B), the central nervous system arises as a solid axis of epiblast cells; the epidermal layer may, however, be carried down into this keel to line the subsequently acquired central lumen; but Shipley denies that this occurs in the Lamprey. This variation has only a secondary significance.

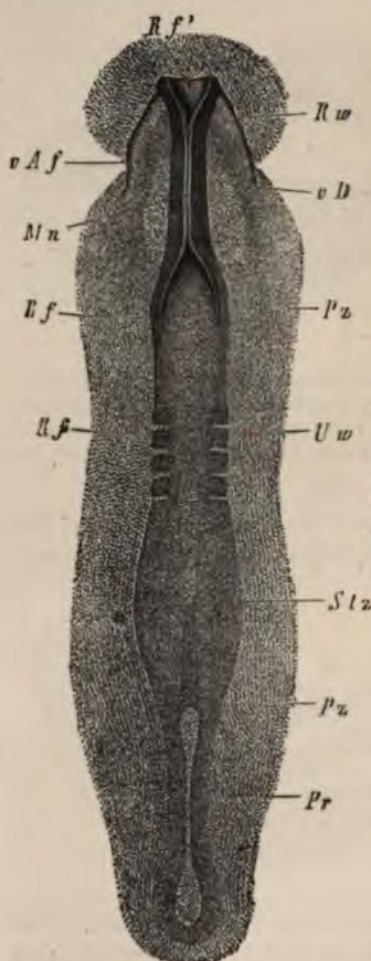


FIG. 100.—EMBRYO FOWL, 3 mm. long, of about twenty-four hours, seen from above, magnified thirty-nine diameters. [From Kölliker].

Ma. union of the medullary folds in the region of the hind-brain; *Pr.* primitive streak; *Pz.* parietal zone; *Rf.* posterior portion of widely open neural groove; *Rf'.* anterior part of neural groove; *Rw.* neural ridge; *Stz.* trunk zone; *vAf.* anterior amniotic fold; *vD.* anterior umbilical sinus showing through the blastoderm.

This divides the embryonic rudiment into a central trunk zone, and a pair of lateral or parietal zones.

In those forms in which the epiblast is early separable into an epidermic and nervous or mucous layer (some Ganoids and Anura) (fig. 24, E), the nervous tract is entirely formed at the expense of the latter, while the epidermal layer of the medullary plate persists as the epithelium of the central canal of the nervous system.

It will be convenient first to trace the further history of the spinal cord and its nerves, and afterwards that of the brain and the cranial nerves. The nervous system at this stage consists of a tube of epiblast several cells thick, with an anterior enlargement (fig. 98). This is practically the adult condition in *Amphioxus*, except that in this form there is no increase in size of the neural canal anteriorly.

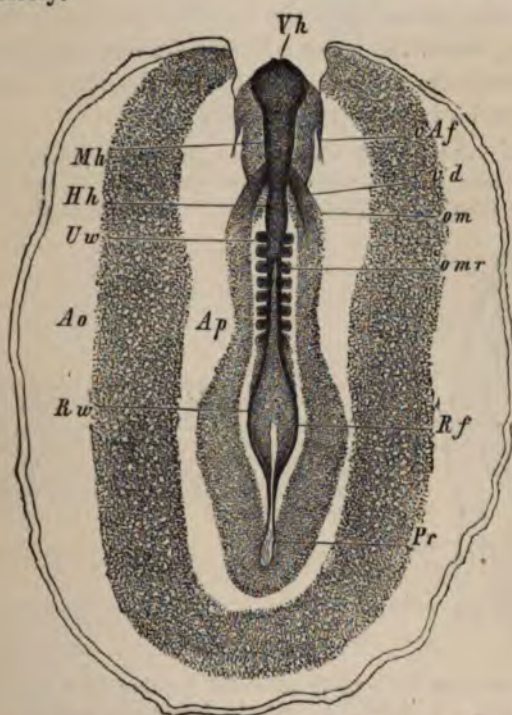


FIG. 101.—EMBRYO FOWL, 4.2 mm. long, of the second day, seen from above, magnified a little over fifty diameters. [From Kölliker.]

Ao. area opaca or vasculosa, bounded by the rudiment of the terminal vessel; the more external portion of this area has not been shaded, and the blood-vessels are not represented; *Ap.* area pellucida; *Ha.* hind-brain; *Ma.* mid-brain; *Vh.* fore-brain; *om.* rudiments of omphalo-mesenteric veins; *omr.* point where the closure of the neural groove is travelling backwards; *Uw.* muscle-plates; other lettering as in fig. 100.

Spinal Nerves.—Immediately after the neural tube has become quite disconnected from the epidermis, paired outgrowths from the dorsal portion of the nervous wall arise at definite intervals (fig. 102). These grow ventral-wards, and are the dorsal (afferent, sensory, or posterior) roots of the spinal nerves. An enlargement, which is apparent very early, is the rudiment of the ganglion. A short time after the appearance of the dorsal roots, the ventral

(efferent, motor, or anterior) roots sprout from the inferior angle of the spinal cord; eventually they fuse with the former.

In *Amphioxus* there are large nerves with dorsal roots, and the ventral roots are represented by a few loose nerve-fibres which do not unite with the former. The ventral roots form distinct nerves in the Marsipobranchs, but in *Myxine* alone are they united with the dorsal into a common trunk.

In a fully developed spinal nerve (fig. 103) a dorsal branch (ramus dorsalis) passes off to the dorsal region immediately below the ganglion; below the latter a branch (ramus intestinalis) passes to the sympathetic system, and finally the main trunk (ramus ventralis) divides into its peripheral branches.

The dorsal roots of the spinal nerves are generally stated to arise from a median dorsal ridge of cells, termed by Marshall the "neural crest." Later, they emerge more from the sides of the spinal cord; and, in some forms, all or some of the



FIG. 102.—TRANSVERSE SECTION THROUGH THE TRUNK OF AN EMBRYO DOG-FISH (*Pristiurus*). [From Balfour.]

al. alimentary canal; ao. aorta; mp. muscle-plate; mp'. portion of muscle-plate converted into muscle; nc. neural canal; pr. dorsal root of spinal nerve arising from the neural crest; sc. somatic mesoblast; sp. splanchnic mesoblast; Vr. portion of the vertebral plate which will give rise to the vertebral bodies; x. subnotochordal rod.

roots on each side are temporarily connected together by a longitudinal commissure (fig. 104). It is possible that the lateral attachment is not, as some investigators believe, an entirely new formation, but that it is due to the upward growth of the dorsal portion of the spinal cord, and the commissures may be each lateral half of the neural crest.

It is, however, conceivable that while the apparent shifting of the attachment of the dorsal roots may primitively be due to the dorsal growth of the spinal cord itself, in some cases, at all events, a second connection due to concrescences may have originated lower down on the sides of the spinal cord.

Sympathetic Nervous System.—The sympathetic ganglia arise, according to Balfour, as enlargements of the main branches of the spinal nerves. Later they are removed from their nerves, but are still connected by short nerves (fig. 103).

Schenck and Birdsell state that in Mammals the main portion of the sympathetic system arises from the lower portion of the spinal ganglia, and that especially in the neck the sympathetic cords arise as a continuous ganglionated chain.

Histogenesis of the Spinal Cord.—When the neural canal is completed, its walls are several cells deep; the thickness increases, and gradually differentiation occurs.

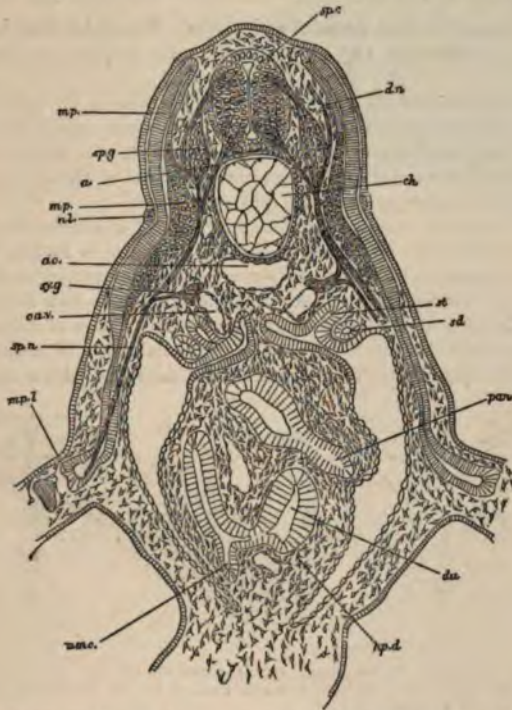


FIG. 103.—TRANSVERSE SECTION THROUGH THE ANTERIOR PART OF THE TRUNK OF AN EMBRYO DOG-FISH (*Scyllium*). [From Balfour.]

As a matter of fact, the ventral nerve roots do not arise immediately below the dorsal but half-way between two dorsal roots.

ao, aorta; ar, ventral root; ca.v, cardinal vein; ch, notochord; du, duodenum; dn, ramus dorsalis; hp.d, point of junction of hepatic duct with duodenum; mp, muscle-plate; mp', part of muscle-plate already converted into muscles; mp.l, part of muscle-plate which gives rise to the muscles of the limbs; nl, nervus lateralis; pan, pancreas; sd, segmental duct; sp.c, spinal cord; sy.g, ganglion of dorsal root; sp.n, spinal nerve; st, segmental tube; sy.g, sympathetic ganglion; umc, umbilical canal.

The peripheral cells lose their cellular appearance, become much elongated in a longitudinal direction forming nerve-fibres. The nerve-fibres are at first non-

FIG. 104.—VERTICAL LONGITUDINAL SECTION THROUGH PART OF THE TRUNK OF A YOUNG SCYLLIUM EMBRYO. [From Balfour.]

ar, ventral (anterior) roots of spinal nerves; com, commissure uniting the dorsal ends of the dorsal nerve-roots; ge, epithelium lining the body-cavity in the region of the future germinal epithelium; pr, ganglia of the dorsal (posterior) roots; sd, segmental duct; st, segmental tubes.



medullated, and occur in greatest profusion in certain definite tracts (white matter), usually ventral or lateral, but soon extending all round the cord. The remaining

primitive cells metamorphose into the nerve-cells of the grey matter, with the exception of those cells which line the central canal, and which always retain their epithelial character.

The nerve-cells are at first rounded and apolar. His states that in the human embryo radial processes arise very early, and that the majority of the cells are at first bipolar.

The central canal retains its primitive slit-like appearance in transverse sections for a long time, but the exact form of the canal in section varies according to the region of the body and age of the embryo. Ultimately it becomes reduced by closure from above downwards to the minute round canal of the adult, which therefore represents the ventral portion of the primitive canal.

The ventral (anterior) fissure is produced by lateral downgrowths of the cord, while the dorsal (posterior) fissure has in the Pig, according to Barnes, the following origin. After the dorsal (posterior) columns of white matter nearly meet one another in the median dorsal line, they grow downwards as two horns (Burdach's tract); in the narrow space between them are wedged two masses of cells (Goll's tract), which are either derived from the cord, or more probably are of mixed origin, *i.e.*, partly mesoblastic (fig. 105). They are separated below by "horn fibres," derived

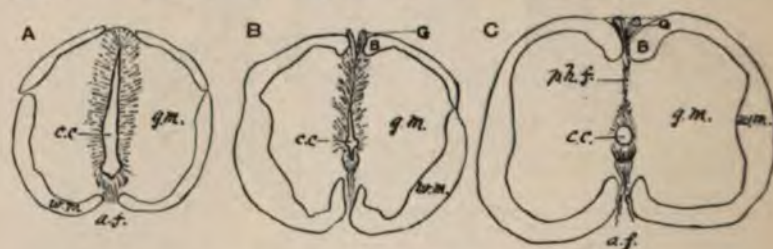


FIG. 105.—DIAGRAMS ILLUSTRATING THE FORMATION OF THE ANTERIOR AND POSTERIOR FISSURES OF THE LUMBAR REGION OF THE SPINAL CORD IN A PIG. [After Barnes.]

A. From an embryo 43 mm. in length.

B. " " 65 " "

C. " " 97 " "

a.f. anterior (ventral) fissure; *B* Burdach's column; *c.c.* central canal; *G* Goll's column; *g.m.* grey matter; *p.h.f.* posterior horn fibres; *w.m.* white matter.

from the degraded epithelial cells of the retreating central canal. The dorsal fissure is thus produced by ingrowths of the dorsal columns of white matter, and the atrophy of the tissue lying between them. The downgrowth appears to be independent of the reduction of the canal, as the latter may be reduced to nearly its minimum length before the former commences (fig. 105, c).

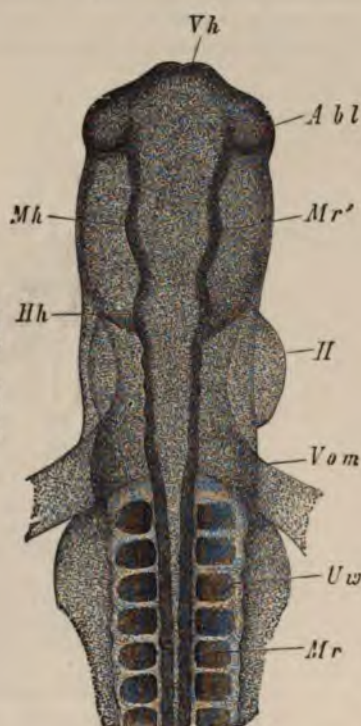
Development of the Vertebrate Brain.—The enlarged anterior portion of the neural canal early exhibits definite dilatations; of these, three primary brain vesicles are usually recognised, the fore-, mid-, and hind-vesicles (fig. 106, *Vh*, *Mh*, *Hh*), but these must not be regarded as having equal morphological value.

The middle-brain vesicle is apparently simple in character, but the last is undoubtedly compound, being formed of several imperfect dilatations, each of which is comparable with the mid-vesicle. The anterior one of these (fig. 106, *Hh*) is always well marked, and dorsally gives rise to the cerebellum.

A noticeable feature in the embryonic brain is the downward curvature of its anterior portion. The flexure is slight in those forms which have small cerebral hemispheres (Cyclostomi, Ganoidae, Teleostei, Amphibia), but well marked in the remaining groups. The "cranial flexure," as it is termed, is apparently rectified as development proceeds, but this is merely due to the increased size of the cerebral hemispheres. The primitive flexure, if anything, becomes more pronounced.

FIG. 106.—DORSAL VIEW OF ANTERIOR PORTION OF EMBRYO FOWL AT THE END OF THE SECOND DAY, 4.27 mm. long. Magnified 40 diameters. [From Kolliker.]

AbL, optic vesicle; *H*, heart; *Hh*, cerebellar dilatation of the primitive brain; *Mh*, mid-brain; *Mr*, neural canal; *Mr'*, wall of mid-brain; *Uw*, transverse-plates; *Vh*, anterior primary brain vesicle; *Vom*, omphalo-mesenteric vein.



Before describing the development of the brain, it will be advisable to give a brief account of the structure of such an unspecialised type of brain as that of the Frog.

The posterior region of the Frog's brain, the medulla oblongata, gradually passes behind into the spinal cord or myelon. It is triangular in shape, with thick side-walls and floor, but the roof is very thin, and richly supplied with blood-vessels forming the choroid plexus. The central canal of the spinal cord expands in the medulla to form the fourth ventricle.

The dorsal anterior wall of this region of the brain is thickened and dorsally produced (fig. 107, *cbl*), and is known as the cerebellum.

The roof of the brain in front of the cerebellum is produced into two thick-walled hollow vesicles, the optic lobes. The cavity of the region of the brain, into which the optic lobes open, is the *iter tertio ad quartum ventriculum* (or passage between the third and fourth ventricle), or more shortly, the *iter*. The anterior end of the

iter is narrowed; in the dorsal wall of this neck lies a transverse bundle of nerve-fibres, the posterior commissure.

The cavity of the brain again expands to form the third ventricle; this brain region is the thalamencephalon. The anterior portion of its roof is prolonged to form the pineal gland, and the posterior portion of its floor forms the sac-like infundibulum, to the extremity of which the pituitary body is attached. A fan-shaped bundle of nerve-fibres passes down the side walls of the thalamencephalon, and decussating on its ventral wall, forms the optic-chiasma (fig. 107, *ac.h*). The median anterior wall of the thalamencephalon is called the lamina terminalis; about half-way up is situated the "anterior commissure" of authors, but this latter is really composed of a separated upper and lower bundle. Osborn has recently shown that the upper bundle (which occurs in all Amphibia and Reptiles) is a rudimentary corpus callosum, as it contains the fibres of the dorso-medial moiety of the hemi-

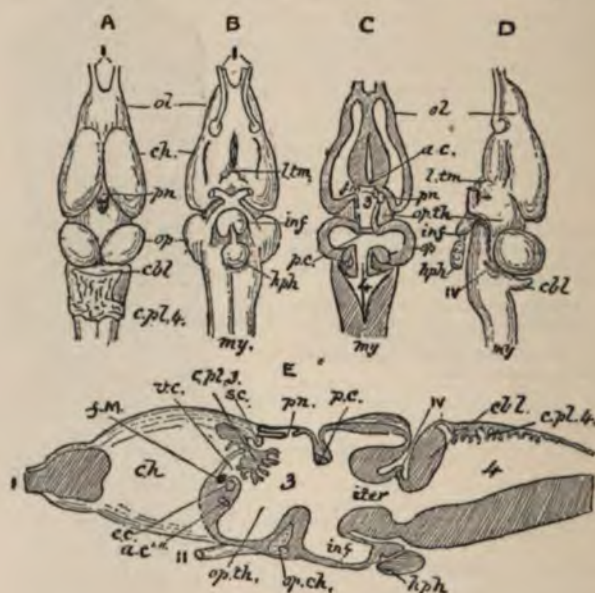


FIG. 107.—BRAIN OF FROG.

A. Dorsal view. B. Ventral view. C. Horizontal section. D. Side view [after Howes]. E. Longitudinal section [after Osborn].

ol, olfactory nerve; *ch*, cerebral hemisphere; *cpl.* 3 and 4, choroid plexus of the third and fourth ventricles respectively; *f.m.*, foramen of Munro; *hph*, hypophysis (pituitary body); *inf*, infundibulum; *iter*, aqueduct of Sylvius; *ltm*, lamina terminalis; *my*, myelon; *op*, optic lobe; *op.ch*, optic chiasma; *op.th*, optic thalamus; *ac*, superior commissure; *i*, olfactory nerve; *ii*, optic nerve; *iv*, fourth cranial nerve; 3 and 4, third and fourth ventricles.

spheres. The lower bundle (Reptiles, Amphibia, Fishes) represents the anterior commissure of Mammals (fig. 109, *Ca*). Two regions are discernible in the lower bundle, the pars olfactoria and the pars temporalis; the latter, feebly developed in the Amphibia, increases with the progressive development of the temporal lobe.

The antero-lateral angles of the thalamencephalon are produced into a pair of elongated lobes, the cerebral hemispheres. They gradually narrow in front, but again slightly enlarge to form the olfactory lobes; from their anterior extremities the olfactory nerves (fig. 107, *i*) pass off to the nose. The olfactory lobes are fused

together in the middle line. The common cavity, lateral ventricle, of each hemisphere and olfactory lobe communicates with the third ventricle through the foramen of Munro.

A diagram of a section of the brain of an embryo Fowl (fig. 108) may be advantageously compared with the Frog's brain. It will be at once noticed that the

FIG. 108.—DIAGRAMMATIC OUTLINE OF A LONGITUDINAL SECTION THROUGH THE BRAIN OF A FOWL EMBRYO OF TEN DAYS. [From Quain after Mihalkovics.]

ac. anterior commissure; amv. anterior medullary velum; below this are the aqueduct of Sylvius and the crura cerebri; ba. basilar artery; bq. corpora bigemina; cai. internal carotid artery; cbl. cerebellum; ch³, ch⁴. choroid plexus of the third and fourth ventricles respectively; h. cerebral hemisphere; inf. infundibulum; lt. lamina terminalis; lv. lateral ventricle; obl. medulla oblongata; olf. olfactory lobe and nerve; opc. optic commissure; pin. pineal gland; pit. pituitary body; ps. pons Varolii; r. roof of fourth ventricle; st. corpus striatum; v³. third ventricle; v⁴. fourth ventricle.



thalamencephalon with the hemispheres and the cerebellum are in this case relatively much larger, and the optic lobes smaller. This is increasingly the case as development proceeds.

A figure of a vertical section through the human brain is given (fig. 109) to illustrate the disproportionate increase in size of the cerebral hemispheres over the rest of the brain, and other Mammalian characteristics.

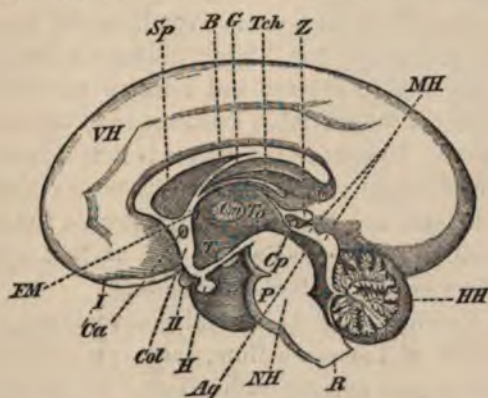


FIG. 109.—LONGITUDINAL SECTION OF AN ADULT HUMAN BRAIN. [From Wiedersheim after Reichert.]

Aq. aqueduct of Sylvius; B. corpus callosum; Ca. anterior commissure; Cm. middle commissure; Col. lamina terminalis; Cp. posterior commissure; FM. foramen of Munro; G. fornix; H. pituitary body; HH. cerebellum; MH. corpora quadrigemina; NH. medulla oblongata; P. pons Varolii; R. spinal cord; Sp. septum lucidum; T. infundibulum; Tch. tela choroidea; To. optic thalamus; VH. cerebrum; Z. pineal gland; I. olfactory lobe and nerve; II. optic nerve.

The Posterior Primary Brain Vesicle.—At first the walls of the hind-vesicle have a fairly uniform thickness (figs. 159, 160), but a noticeable change occurs when the above-mentioned anterior thickening (cerebellum) increases in size. The side walls of the posterior multiple division, **medulla oblongata**, become much

thickened and grow away from each other dorsally, leaving a very thin roof which possesses but little nervous tissue (figs. 125, 126). In transverse sections the medulla at this stage has a very characteristic triangular outline (figs. 112, 126).

The side walls and floor of the medulla become greatly thickened, and local enlargements form the olivary bodies and pyramids. The thin roof of the cavity of the medulla, fourth ventricle, soon becomes very vascular, and is known as the choroid plexus of the fourth ventricle.

The minor enlargements of this region of the brain alluded to above disappear very early and leave no trace.

The **Cerebellum** at first appears as a thickened anterior dorsal border to the medulla; in many types this undifferentiated condition is practically retained throughout life (Marsipobranchs, some Ganoids, Dipnoi, Amphibia, and some Reptiles). In other forms the roof becomes greatly enlarged; in Elasmobranchs the cerebellum is relatively very large, and at an early stage appears to be composed of two lateral halves. In Birds a central lobe appears and grows to a very large size; the walls being much folded, constitute what is termed an *abor-vitæ*; there are two small lateral lobes or *flocculi*. In the development of the higher Mammals the central lobe (*vermis*) is the first to appear, and remains relatively large for some time, but the lateral lobes (*hemispheres*) usually eventually dwarf the former. In connection with this it is interesting to note that the cerebellum in the Monotremes consists almost entirely of the median lobe, and that in the Marsupials the lateral lobes are still small. The cerebellar fissures at first appear on the *vermis* and then extend to the *hemispheres*.

The *Pons Varolii*, being the ventral commissure connecting the two *hemispheres* of the cerebellum, has a proportionate development with them, and appears rather late. In the Monotremes it is scarcely more developed than in many *Sauropsida*.

The Middle Primary Brain Vesicle.—The mid-vesicle, or, as it is usually termed, the mid-brain, has a much simpler history than the other regions of the brain. The cavity always remains small, and is known as the *Aqueductus Sylvii* or *iter a tertio ad quartum ventriculum*. In most of the lower Vertebrates the roof is produced into two vesicles, the optic lobes or *corpora bigemina* (fig. 107, *op*). In Birds these assume a lateral position, and the roof of the mid-brain is thin. In Mammals the roof gives rise to the solid *corpora quadrigemina* (fig. 109).

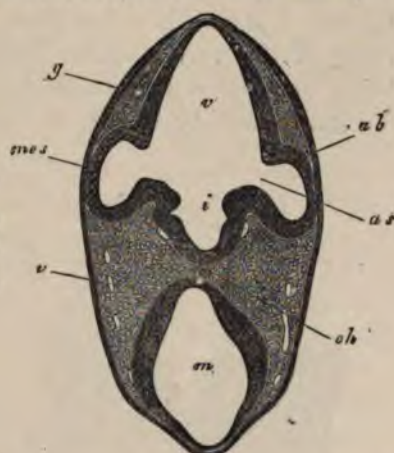
In an early stage of their development in Mammals the corpora quadrigemina are said to appear as an indistinct pair of lobes, a phase comparable with the optic lobes (corpora bigemina) of the lower Vertebrates. But Kölliker states that the anterior pair are at first separated from one another by a short longitudinal groove and only partially from the posterior undivided mass. Later the posterior bodies are completed by a meeting of the lateral grooves and a posterior extension of the median groove. In the Monotremes the anterior bodies are well marked, the posterior being inconspicuous, and, according to Owen, not separated by a median groove.

The floor of the mid-vesicle is greatly thickened, and forms the *crura cerebri*. The relative size of this section of the brain is very much greater in the embryo than in the adult.

The Anterior Primary Brain Vesicle.—The primitively single cavity of the fore-vesicle is very early produced into a pair of lateral vesicles, the optic vesicles (figs. 106, 110), the further history of

FIG. 110.—HORIZONTAL SECTION OF THE BRAIN OF A RABBIT OF TEN DAYS. Magnified 40 diameters. [From Kölliker.]

ab. mesoderm; *as.* peduncle of optic vesicle (33 μ diam.); *ch.* notochord; *g.* thickening of the epiblast in the region of the future olfactory pits; *i.* infundibulum; *m.* mid-brain; *mes.* optic vesicle (26 mm. high); *v.* anterior brain vesicle; *v.* veins.



which is connected with the development of the eye (pp. 157-167). The fore vesicle grows anteriorly, and a small downgrowth from the roof indicates the distinction between the anterior and posterior divisions of the fore-brain. The posterior division is the **thalamencephalon** (figs. 111-115); the anterior will give rise to the cerebral hemispheres and olfactory lobes.

The anterior portion of the floor of the thalamencephalon thickens to form the optic chiasma, while the posterior part is produced into a blind backwardly directed pouch, the infundibulum (figs. 110, 115, 135).

In the lower Vertebrates the infundibulum is usually relatively large, but in the higher forms it is much reduced. In Teleostei ventral-lateral swellings of the infundibulum constitute the lobi inferiores; the single tuber cinereum of Mammals occupies a similar position. The corpus albicans, which is single in the lower Mammals, but double in Man and the higher Apes, though single when first developed, arises behind the infundibulum.

The pituitary body (figs. 107, *hph*; 109, *H*; 112, *hp*; 116, *hph*) (hypophysis cerebri) becomes more or less intimately connected with the fundus of the infundibulum, but it is in nowise a nervous structure (see p. 100).

The walls of the thalamencephalon greatly increase in thickness, and form the optic thalami (fig. 111). The middle or soft com-

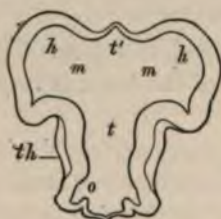


FIG. 111.—HORIZONTAL SECTION OF ANTERIOR PORTION OF THE BRAIN OF AN EMBRYO SHEEP, 15 mm. long. Magnified 5 diameters. [From Kölliker.]

h, cerebral hemispheres; *m*, position of the future foramen of Munro; *o*, recess which, deeper down, passes into the optic nerve; *t*, third ventricle; *t'*, central portion of thalamencephalon, in front is the lamina terminalis; *th*, optic thalamus.

missure of Mammals unites these structures anteriorly across the cavity of this region of the brain (third ventricle). It is probably homologous with a commissure described by Balfour in Elasmobranchs, and by Osborn in Amphibia (supra-commissura) (fig.

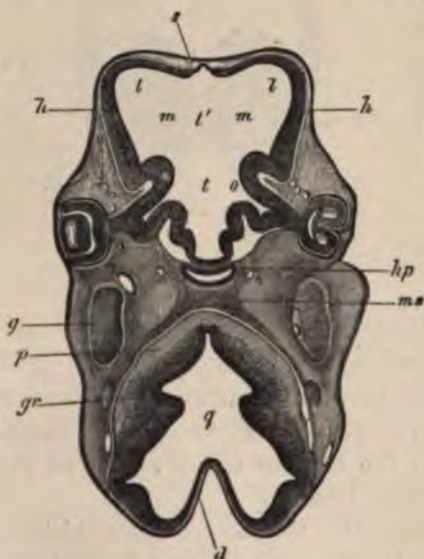


FIG. 112.—HORIZONTAL SECTION OF THE HEAD OF AN EMBRYO SHEEP, 15 mm. long. Magnified 50 diameters. [From Kölliker.]

d, thin roof of fourth ventricle *g*; *g*, Gasserian ganglion; *gr*, nerve-cells in floor of fourth ventricle; *h*, cerebral hemisphere; *hp*, hypophysis (pituitary body); *l*, lateral ventricle; *m*, position of future foramen of Munro; *ms*, axial portion of skull; *o*, cavity of optic stalk; *p*, nerve-fibres of pyramid; *s*, lamina terminalis; *t*, posterior and deeper portion of third ventricle; *t'*, anterior portion of the same.

107, *s.c.*), which crosses the roof of the third ventricle immediately in front of the pineal gland.

The **pineal gland**, or epiphysis cerebri, develops as a diverticulum from the roof of the third ventricle (figs. 107–109, 116). It usually becomes a long narrow tube, the lumen of which may persist throughout life, but usually the proximal end atrophies to a

thread-like stalk, while the distal portion is enlarged, and becomes lobular or branched. The enlarged termination may remain outside the cranium (Raja and Anura) or become imbedded within it (Acanthias and some Lizards), but in most cases it lies beneath the roof of the skull. In Elasmobranchs and some Urodela the pineal gland retains its sac-like character (fig. 138*, B).

Ahlborn regards the pineal gland as the rudiment of a primitive unpaired eye, from its position, origin, and mode of development, and compares it with the unpaired eye of *Amphioxus* and larval *Ascidians*. This view has since been confirmed by De Graaf, who has shown that in *Anguis* the epiphysis has the structure of an eye constructed on the invertebrate plan. Spencer has still more recently extended this discovery to *Hatteria* and other Lizards (fig. 138*, c-e). This organ is lodged within the parietal foramen. A similar foramen is found in the skulls of *Labyrinthodonta* and certain extinct *Reptilia*, and also, as Osborn has pointed out, in the Mesozoic Mammal *Tritylodon* (see also p. 162).

Behind the pineal gland the optic thalami are further connected across the roof of the brain in the Elasmobranchii, Amphibia (fig. 107, *p.c*), Sauropsida, and Mammalia (figs. 109, *Cp*; 116, *p.com*) by a transverse commissure, the posterior commissure. This is always situated at the base of the posterior peduncle of the pineal gland.

In front of the pineal gland the greatly thinned roof of the third ventricle, *velum interpositum*, becomes very vascular, and forms the choroid plexus of the third ventricle or *tela choroidea* (figs. 107-109, 116, *ch.p* 3).

The **cerebral hemispheres** usually arise as a pair of lobes from the roof of the anterior or cerebral portion of the fore-brain, each containing a cavity, lateral ventricle, which is continuous with that of the central nervous system (figs. 107, 108, 111, 112).

That portion of the fore-brain lying in the median line between the cerebral hemispheres is the *lamina terminalis* (figs. 108, 116, *lt*), and it extends from the roof of the *thalamencephalon* to the optic chiasma.

The Y-shaped passage connecting the lateral ventricles with the third ventricle is the primitive foramen of Munro. Though at first wide (fig. 111, *m*), it is ultimately greatly narrowed (fig. 109, *F, M*).

There is throughout the Vertebrate series considerable diversity in the size and structure of the cerebral hemispheres. Their condition in the Amphibia has already been described.

The cerebral hemispheres show a marked increase in size in the Sauropsida, and reach their culminating point in the Birds; but

even here they attain a low stage of evolution as compared with the hemispheres of the Mammalia.

Not only do the cerebral hemispheres in Mammals grow forward, but they extend backward so as to hide the thalamencephalon and the mesencephalon in a dorsal view, and even project beyond the cerebellum in Man (fig. 109) and the higher Apes. The com-



FIG. 113.—LATERAL VIEW OF THE BRAIN OF AN EMBRYO CALF OF 5 CH. [From Balfour after Mihalkovics.]

The outer wall of the hemisphere is removed, so as to give a view of the interior of the left lateral ventricle.

am, hippocampus major (cornu ammonis); cb, cerebellum; d, choroid plexus of lateral ventricle; fm, foramen of Munro; ia, cut wall of cerebral hemisphere; ia, infundibulum; mb, mid-brain; op, optic tract; pa, pons Varolii, close to which is the fifth nerve with the Gasserian ganglion; st, corpus striatum; IVV, roof of fourth ventricle.

plexity of this region of the adult brain is due to local thickening, reduction, infolding, and fusion.

The external walls of the primitively simple cerebral hemispheres become greatly thickened, while the inner walls—i.e., those in contact with one another in the median line—are extremely thin.

The mesoblastic sheath surrounding the developing brain grows downwards as a lamina into the longitudinal fissure between the



FIG. 114.—BRAIN OF A HUMAN EMBRYO OF SIX MONTHS. Natural Size. [From Kölliker.]

c, cerebellum; f, foculus; fs, fossa Sylvii; a, olivary body; ol, olfactory bulb; p, pons Varolii.

hemispheres. From this will be derived the falx cerebri and the choroid plexus (fig. 115, *f* and *pl*).

The floors of the hemispheres become much thickened and constitute the corpora striata. These protrude so much into the lateral ventricles as to cause them to assume a curved appearance in a longitudinal vertical section (fig. 113, *st*), thus constituting the anterior and posterior cornua of the lateral ventricles.

The position of the corpus striatum is indicated in an external side view of a cerebral hemisphere by the fossa Sylvii (fig. 114, *fs*), which demarcates the frontal and temporal lobes.

Owing to their backward extension, the corpora striata become increasingly connected with the optic thalami (fig. 115, *st*, *th*), with which they ultimately fuse so completely that the line of separation cannot be recognised.

The corpora striata are connected together by the anterior commissure which traverses the anterior wall of the third ven-



FIG. 115.—TRANSVERSE SECTION OF THE BRAIN OF AN EMBRYO SHEEP, 2.7 cm. long. Magnified 10 diameters. [From Kölliker.]

a. cartilago of orbito-sphenoid; *e.* peduncular fibres; *ch.* optic chiasma; *f.* median cerebral fissure; *h.* cerebral hemispheres, with a convolution upon their inner wall projecting into the lateral ventricles, *l.*; *m.* foramen of Munro; *o.* optic nerve; *p.* pharynx; *pl.* lateral plexus; *a.* termination of the median fissure which forms the roof of the third ventricle; *sa.* body of the anterior sphenoid; *st.* corpus striatum; *t.* third ventricle; *th.* anterior deep portion of the optic thalamus.

tricle. This is the earliest developed commissure which connects the cerebral hemispheres, and is found, though of smaller size, in the Sauropsida and Ichthyopsida. It lies in the substance of the lamina terminalis (figs. 107-109, 116 *a.c.*).

The inner wall of each hemisphere projects into its lateral ventricle as two longitudinal ridges extending from the foramen of Munro to nearly the posterior end of the descending cornua. The upper one, hippocampus major or cornu ammonis (figs. 113, *am*; 115, *h*), is a solid nervous structure, while the lower ridge is very thin and folded, and by the ingrowth into it of a large number

blood-vessels from the falx forms the choroid plexus of the lateral ventricles (figs. 113, *d*; 115, *pl*).

The cerebral hemispheres of Mammals unite with one another in front of and above the lamina terminalis; the fused internal walls being very thin, are termed the septum lucidum or septum pellucidum (figs. 109, *Sp*; 116, *s.l*). In Man the two walls enclose a slit-like cavity, the so-called fifth ventricle. As this space is really only a portion of the longitudinal fissure between the hemispheres enclosed by overgrowth, it, morphologically speaking, lies outside the brain, and consequently is not lined by an epithelium, like the true ventricles.

The fornix (fig. 116, *fx*) is a band of nerve-fibres which unites the hemispheres along the inferior border of the septum. In front it divides into two anterior pillars or columns, each of which, passing in front of the foramen of Munro and behind the anterior

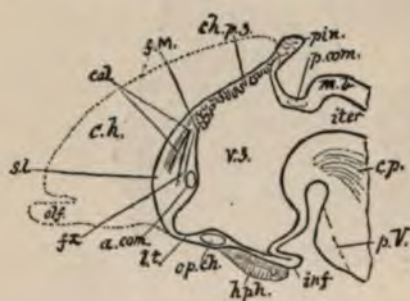


FIG. 116.—LONGITUDINAL VERTICAL SECTION THROUGH THE ANTERIOR PART OF THE BRAIN OF AN EMBRYO RABBIT OF 4 CELLS. [After Mihailovics.]

a.com. anterior commissure; c.h. cerebral hemisphere; c.p. cerebral peduncles; c.c. corpus callosum; ch.p. choroid plexus of the third ventricle; f.m. foramen of Munro; fx. fornix; h.p.h. hypophysis (pituitary body); inf. infundibulum; iter. aqueductus; l.t. lamina terminalis; m.b. mid-brain; ol. olfactory lobe; op.ch. optic chiasma; p.com. posterior commissure; pin. pineal gland; p.V. pons Varolii; s.l. septum lucidum; V.3. third ventricle.

commissure, terminates in the corpus albicans (or in each of the two corpora in Man). Behind, the fornix also divides into two posterior pillars or crura, each of which eventually passes into the hippocampus major in the descending cornu of the lateral ventricle of its side.

The characteristic commissure of the Mammalia, the corpus callosum, arises last of all in the upper portion of the septum lucidum, and serves to directly connect the two cerebral hemispheres. The curved anterior section (genu) is the first portion to develop, and this alone occurs in the Monotremata and Marsupials; in these groups the anterior commissure is relatively very large. The corpus callosum keeps pace with the hemispheres as they increase in size and extend backwards. As was stated on p. 124 a rudiment of the corpus callosum is found in Amphibia and Reptiles.

In the lower Vertebrates the cerebral hemispheres are smooth throughout life, but in the higher Mammals the surface of the hemispheres is thrown into a number of folds (convolutions) with deep grooves, or sulci between them.

Kölliker was the first to distinguish two kinds of cerebral convolutions and sulci, which he now terms primitive and secondary. The former appear early, and all but disappear long before birth. The sulci are the expression of actual infoldings of the walls of the hemispheres, and correspond with those local thickenings which constitute such structures as the corpus striatum, hippocampus major, &c. The sulcus of the first of these (fig. 114, *fs*) is the only one which markedly persists throughout life.

The secondary convolutions begin to appear about the middle of foetal life in Man. They affect only the more superficial portion of the cerebral walls, and probably originate by arrest of growth in the sulci, accompanied by active growth in the convolutions; the arrest of growth may be partly induced by the pressure of the main blood-vessels of the hemispheres.

In many of the lower Mammals the cerebral hemispheres are smooth, *i.e.*, free, or nearly so, from the secondary convolutions. The order of the appearance of the convolutions is too special a subject to be dealt with here; but, speaking in general terms, the cerebral convolutions of the brains of certain adult Lemurs and Monkeys correspond with stages observed in the development of the human brain.

The **olfactory lobes** (Rhinencephala) usually arise as hollow prolongations from the antero-ventral end of the cerebral hemispheres (figs. 107, 108, 116). According to Marshall, they arise in Elasmobranchs (fig. 120, *ol.v*) and Birds after the appearance of the olfactory nerves. They are relatively large in the adults of low forms, and in the embryos of the higher Mammals.

In all Mammals the olfactory lobes are at first hollow, the cavities being prolongations of the lateral ventricles; in Man the lobes become solid and quite small (figs. 109, 1; 114, *ol*). In the lower Mammals they constitute the anterior extremity of the brain; but owing to the forward growth of the cerebral hemispheres in the higher Mammals, they eventually occupy a ventral position.

The envelopes of the brain are entirely of mesoblastic origin.

Summary of the History of the Mammalian Brain.—The primitive neural tube dilates to form certain vesicles, all of which have not the same morphological value. They may be thus tabulated :—

Primary Vesicles.	Secondary Vesicles.	Huxley.	Wilder, "Quain."
Anterior or Fore-Vesicle	Fore-brain*	Prosencephalon	Prosencephalon
	Inter-brain or	Thalamencephalon	{ Thalamencephalon or Diencephalon
	"Tween-brain }		
Middle or Mid-Vesicle	Mid-brain	Mesencephalon	Mesencephalon
Posterior or Hind-Vesicle	Hind-brain	Metencephalon	Epencephalon
	After-brain	Myelencephalon	Metencephalon

The greater portion of the walls of these primitive vesicles become enormously thickened, thus the anterior portion of the roof of the hind-vesicle (hind-brain) forms the cerebellum, and the floor and sides develop the olivary bodies, pyramids, &c., and anteriorly the pons Varolii.

The corpora bigemina (or quadrigemina) are developed from the roof of the middle vesicle, and the crura cerebri from the floor.

In the anterior vesicle, the floor of the thalamencephalon develops the corpus albicans and optic chiasma, and the walls of the optic thalami. The floor of each half of the prosencephalon (cerebral hemispheres) develops the corpora striata, and the inner walls the hippocampus major; the external walls are greatly thickened.

But portions of the primitive vesicles remain thin and develop vascular plexi; these are :—The roofs of the myelencephalon (medulla) and thalamencephalon, and part of the inner walls of the prosencephalon.

The cerebral hemispheres grow backward, and their lateral vesicles are considerably altered in shape and their cavities reduced by the ingrowth of the walls and floor; as, for example, the hippocampi and corpora striata.

The lateral elements of the brain are co-ordinated by the development of transverse commissures, of which the following are the most important :—Pons Varolii for the cerebellum, posterior commissure, anterior portion of the roof of the mesencephalon, middle commissure across the third ventricle, and the anterior commissure in its front wall. This, with the fornix at the base of the septum lucidum and the corpus callosum above it, serve to directly connect the cerebral hemispheres with each other. The decussation of the fibres of the optic chiasma, strictly speaking, come under this head.

The Cranial Nerves.—The dorsal roots of the cranial nerves, like those of the spinal nerves, arise from the dorsal portion of the cerebro-spinal axis. A neural crest, continuous with that of the spinal cord, is probably always present.

Most of the cranial nerves are usually regarded as homologous with the spinal nerves, and as having a segmental significance, but

* Corresponding to the German Vorderhirn, Zwischenhirn, Mittelhirn, Hinterhirn, and Nachhirn.

considerably modified, owing to the great changes which have taken place in the cephalic region.

The following is a brief summary of what is known concerning the development of the cranial nerves. The numeration and terminology is that which is usually adopted by anatomists.

XII. and XI. The Twelfth or Hypoglossal, and the Eleventh or Spinal Accessory Nerves.—Neither of these nerves is constant as a cranial nerve throughout the vertebrate series. For the present they may be dismissed, as they are regarded by some as belonging to the spinal series (see p. 141). Their development is not well known.

X. The Tenth or Vagus Nerve.—The tenth nerve arises from the neural ridge in the myelencephalon (medulla) behind the audi-



FIG. 117.—DIAGRAM ILLUSTRATING THE GENERAL DISTRIBUTION OF THE CRANIAL NERVES.
[Modified from Beard.]

A-C. The three anterior head-cavities. L-X. The cranial nerves (ordinary numeration).

au., auditory vesicle; b1-b7, seven branchial clefts; ci, ciliary ganglion; h, hyoid cleft; int, intestinal branch of vagus nerve; m, mouth; olf, olfactory pit; oph. v. and vii, ophthalmic division of the trigeminal and facial nerves respectively; oph. prof, ophthalmic profundus; pal, palatine branch of the facial nerve. The radix longa unites the ciliary with the Gasserian ganglion (v.).

tory involution; it soon develops a large ganglion, beyond which it is produced as the intestinal branch. Later several anterior roots arise from the ventral surface of the brain and join the vagus. This nerve sends a pair of branches to supply the two sides of the posterior branchial (visceral) clefts (see p. 177). In the Marsipobranchii, and in Notidanus, the last six of the seven branchial clefts are supplied by this nerve; in other Vertebrates the number is less. Thus the tenth nerve is usually regarded as equivalent to at least six segmental nerves, the single origin of the tenth nerve being supposed to be of secondary significance. For several reasons *Amphioxus* cannot be utilised for comparison, one being that there is no correspondence between the number of the body segments and branchial clefts in that form.

IX. The Ninth or Glosso-Pharyngeal Nerve.—The ninth nerve usually has a common origin with the tenth nerve, but it very soon becomes distinct, and, like the latter, it acquires numerous roots. This nerve passes immediately behind the auditory capsule and expands above the first branchial cleft into a ganglion. From the latter a thick posterior branch is distributed to the anterior border of the first branchial arch, and a thinner branch to the posterior border of the hyoid arch.

VIII. The Eighth or Auditory Nerve.—The eighth nerve (fig. 126, E, VIII) arises in such close contiguity with the seventh that it is usually stated to be a branch of it; but Beard maintains that it is a true segmental nerve. It is a short thick nerve with a large ganglion, and is solely the sensory nerve of the ear.

VII. The Seventh or Facial Nerve.—The seventh nerve early develops as an outgrowth from the neural crest on the dorsal surface of the myelencephalon just in front of the auditory capsule. At an early stage it acquires a new or secondary attachment to the side of the brain; but, unlike any other nerve, cranial or spinal, the original or primary root is retained as well as the secondary [Marshall]. The main branch of this nerve passes down the anterior side of the hyoid arch (p. 178); a smaller branch (præspiracular) forks over the hyomandibular cleft (spiracle); in Mammals it joins the mandibular division of the fifth nerve, and is known as the chorda tympani. The seventh nerve also gives rise very early to two anterior branches, the upper (portio facialis of the ophthalmicus superficialis) passes to the front end of the head along with the ophthalmic division of the fifth nerve. The lower or palatine (superficial petrosal of Mammals) runs superficially to the superior maxillary division of the fifth.

VI. The Sixth or Abducent Nerve.—The sixth nerve arises from the median ventral line of the brain below the seventh nerve, and never develops ganglion cells. It is an exclusively motor nerve, which supplies the rectus externus muscle of the eyeball, and also in some forms the retractor muscle of the bulb of the eye and the nictitating membrane.

V. The Fifth or Trigeminal Nerve.—The fifth nerve develops from the neural ridge in front of the seventh nerve. After expanding into a large ganglion (Gasserian ganglion), it arches over the mouth, the main trunk (mandibular or inferior maxillary) being distributed over the lower jaw, and the smaller (superior maxillary) over the upper jaw. The dorsal division of the fifth nerve emerges

anteriorly from the Gasserian ganglion, and follows the ophthalmic division of the seventh nerve to its distribution at the anterior end of the head; it is known as the *portio profunda* or *minor* of the *ophthalmicus superficialis*. A nerve connecting the Gasserian with the ciliary ganglion is usually termed the ophthalmic division of the fifth nerve; it appears not to be a branch of that nerve.

IV. The Fourth, Pathetic or Trochlear Nerve.—In its earliest recognised condition the fourth nerve has the same position that it occupies in the adult, viz., the dorsal surface of the extreme hinder border of the mid-brain. It invariably innervates the superior oblique eye-muscle, and in many Vertebrates sends sensory branches to the conjunctiva and the skin of the upper eyelid.

III. The Third or Oculomotor Nerve.—Marshall thinks it is probable that the third nerve grows from the neural crest on the top of the mid-brain; but as in the adult it arises very near the mid-ventral line, it must undergo the maximum amount of change of position. But Beard states that the nerve described by Marshall is really the *radix longa*, and believes, though he has no direct evidence to give, that the oculomotor does not arise from the neural crest. This nerve is associated with the ciliary or ophthalmic ganglion, and is distributed to all the muscles of the eyeball except those supplied by the fourth and sixth nerves, as well as to the levator palpebræ superioris and the circular muscles of the iris.

II. The Second or Optic Nerve.—The second nerve is merely a degenerate portion of the brain itself, being the stalk of the optic vesicle (p. 160).

I. The First or Olfactory Nerve.—The first nerve arises from the dorsal part of the sides of the anterior cerebral vesicle before the cerebral hemispheres have commenced to develop. Owing to the enormous development of the latter in the higher Vertebrates, the nerve comes to occupy a ventral position. It is exclusively distributed to the nasal fossæ (figs. 117, 120, 1).

Hypotheses concerning the Segmental Value of the Cranial Nerves.—Recently both Spencer and Beard have shown that after the (dorsal) roots of the cranial nerves arise from the neural ridge, they fuse with the epiblast at the level of the notochord. The epiblast cells at these spots proliferate the masses of cells thus developed, forming the cranial ganglia; and at the same time a rudimentary structure is formed, termed by Beard the branchial sense organ, and by Spencer the sense organs of the lateral line in the head. As these organs at first only appear in the gill-bearing region of the body, the former term is perhaps the preferable.

Miss Johnson and Miss Sheldon, who have still more recently investigated the development of the cranial nerves in the Newt, admit the fusion of the cranial nerves with the incipient serial sense organs (mucous canals or lateral line organs of the head). They deny that the ganglion is derived from this fusion, but state that it takes its origin from the original outgrowth from the neural ridge, as Redot has also shown for the spinal nerves in Triton.

Beard states that the dorsal root of a cranial nerve develops in the following manner. The nerve grows downwards from the neural ridge below, but unconnected with the epiblast. About the level of the notochord it fuses with the epiblast, but part of the nerve passes on to the lateral muscle-plates of the segment (fig. 118); this main or posterior branch (post-branchial nerve) of Beard, chiefly innervates the gill-muscles. Proliferation at the junction of the nerve with the epiblast gives rise to the ganglion of the dorsal root, and externally to the rudiment of the primitive branchial sense organ of that root. As the ganglion separates from the skin a nervous tract is left, the so-called dorsal branch (supra-branchial nerve). The anterior or prebranchial nerve, and probably the pharyngeal branch, are also derived from this proliferation.

Following up this discovery, Beard has attempted a re-enumeration of the seg-

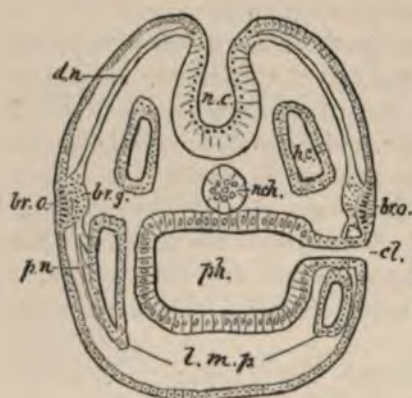


FIG. 118.—DIAGRAMMATIC TRANSVERSE SECTION THROUGH THE GILL-BEARING REGION OF AN ELASMOBRANCH OR OTHER ICHTHYOPSID. [After Beard.]

Neural canal not yet closed over. On the left side the gill muscle-plate is shown, and on the right the gill cleft.

br.g. branchial ganglion; br.o. branchial sense-organ; cl. visceral cleft; d.n. dorsal (posterior) root of segmental nerve; h.c. head-cavity; l.m.p. lateral muscle-plate; n.c. neural canal; nch. notochord; ph. pharynx; p.n. post-branchial nerve.

ments of the head, and a review of the nature of the nerves themselves. The following is briefly his position.

The ganglia known to human anatomists as the olfactory bulbs, ciliary, Gasserian, geniculate, auditory, petrous, and pneumogastric ganglia, all belong to the same series, and are associated with primitive sense organs. The table given on p. 140, when compared with fig. 117, will elucidate their relationships, and but few remarks will be necessary.

On this hypothesis the nerves arising from the cranial neural crest and uniting with the primitive sense organ of its segment correspond to some extent with the dorsal branches of the spinal nerves. The nerves and their ganglia are: (1) the olfactory nerve and ganglion; (2) the radix longa (or the nerve uniting the ciliary with the Gasserian ganglion) and the ciliary ganglion; (3) the trigeminal nerve and the Gasserian ganglion; (4) the facial nerve with its ganglion; (5) the auditory nerve and ganglion; (6) the glosso-pharyngeal nerve and its ganglion; (7+) the vagus nerve with its segmental branches and their associated ganglia.

The association of the dorsal root of the ciliary nerve (radix longa) with the Gasserian ganglion, instead of its directly arising from the brain, is explained by Beard as being due to the primitive outgrowths being very close together.

The oculomotor (III.), trochlear (IV.), and abducent (VI) nerves are regarded as the anterior roots of the *radix longa* (ciliary), trigeminal (V.), and facial (VII.) nerves respectively. They all supply the eye-muscles, the latter being developed from the first two († three) head cavities.

The fact that there are two anterior branches (ophthalmic and palatine) of the seventh nerve, is one reason for supposing that there may be a missing head segment between the third and fourth of the above enumeration. Independently of this, there are two pre-oral segments; and counting the auditory as a true segment, there are nine post-oral in the Fish, with the greatest number of gill-clefts (Notidanus). This makes a total of at least twelve segments in the Vertebrate head.

Little need be added concerning the segmental sense organs, as they usually at first appear as patches of columnar cells lining a slight depression of the epidermis.

Serial Cranial Sense Organs.—The organs of the lateral line consist of a series of mucous canals containing groups of sense-cells which are segmentally disposed in the trunk (see p. 148). The canals are variously distributed in the head, but in the body they almost invariably extend along the middle line of each side, as far as the tail. This system of sense organs is only found in Fishes, Urodele Amphibia, and the larvæ of the Anura.

In the head the canals are innervated by cranial nerves, the lateral line proper being supplied by the lateral branch of the vagus.

The lateral line itself is developed from a backward growth of the epiblastic proliferation, which gives rise to the sense organ of the vagus. This ploughs its way along the superficial epiblast and the indifferent epiblast cells, which are thus thrust aside and are probably lost [Beard] (fig. 103).

As in other cases, the nerve of the sense-organ is formed from the deeper layer of the sensory thickening.

The extension of these (primitively branchial) sense organs to the hinder end of the body is supposed by Beard to be of only secondary significance. Some authors, however, believe that the connection of the (segmental) organs of the lateral line with the vagus is itself secondary.

Of the primitive segmental sense organs, the first has become retained and modified as the olfactory organ. In most Ichthyopsida the organs of the lateral line of the head are still innervated by certain cranial nerves (ciliary, trigeminal, facial, and glosso-pharyngeal). The auditory organ may possibly be a highly specialised segmental sense organ, its histological structure also lending support to this view. The posterior organs persist as the organs of the lateral line of the body in the Ichthyopsida.

The presence of primitive branchial sense organs is not confined to the Ichthyopsida. Froriep has discovered rudiments of them for the facial, glosso-pharyngeal, and vagus segments in Cow and Sheep embryos; and Beard finds them in the Fowl for the ciliary and trigeminal, in addition to the above segments. In all cases they disappear very soon.

Thymus Gland.—The paired serial rudiments of the thymus gland arise in a manner which is very suggestive of their having possessed a primitive branchial sensory function. For the sake of convenience the development of this composite gland will be described in another section (p. 184).

The primitive branchial clefts suffer great reduction. The more or less rudimentary hyoidean cleft (spiracle) is lost in the Teleosts. Most Fishes have but five true branchial clefts. The absolute extinction of the branchial clefts is well exhibited in the higher adult Urodele Amphibia; but in these and in all higher animals the hypoblastic evagination concerned in the hyoid cleft more or less persists as the Eustachian tube or recess (p. 180).

TABLE OF CRANIAL SEGMENTS AND THEIR NERVES AND SENSE-ORGANS.
[Slightly modified from Beard.]

Segment.	Dorsal Nerve Root.	Cleft.	Nature of Sense Organ of Cleft.	Ganglion.	Supra-Branchial Nerve.	Head Cavity.	Ventral Nerve Root.
I.	Olfactory	†	Olfactory organ	Olfactory	None	None	None
II.	Radix longa	†	Branchial †	Ciliary	Ophthalm. prof.	First	Motoroculi
III.	Trigeminal	Mouth	Branchial	Gasserian	Ophthalm. superf.	Second	Trochlear
IV.	Facial	Absent.	Branchial	Facial }	Portio facialis of ophthalm. superf.	Third	Abducens
V.		Hyoid or spiracle	Branchial				
VI.	Auditory	None	Auditory organ	Auditory	None	None	None
VII.	Glossopharyngeal	Branchial, 1	Branchial	Glossophar.	Sup. temp.	†	None
VIII.	Vagus, 1	Branchial, 2	Branchial	Vagus, 1	Sup. temp.	None	None
IX.	Vagus, 2-6 (Heptanchus)	Branchials, 3-7	Branchial	Vagus, 2-6	Lateral nerve	None	None
X.							
XI.							
XII.							
XIII.							

This table will be found to differ from fig. 117 in having two hyoid segments, and consequently in accounting for a total of thirteen segments. The first segment corresponds with the fore-brain vesicle, the second with the mid-vesicle, and the remainder with the hind region of the brain.

Froriep divides the Mammalian head into three regions:—(1) prepituitary or trabecular, with the nose and eyes; (2) pseudo-vertebral, with the trigeminal, facial, glosso-pharyngeal, and composite vagus nerves, which supply the pharyngeal clefts; (3) vertebral, consisting of the occipital bone and hypoglossal nerve. He has found that in the embryos of Ruminants there are rudiments of three distinct protovertebræ in front of the first cervical (spinal) nerve and behind the vagus. In front of each of these rudiments ventral nerve roots arise, which all unite in a single trunk, the hypoglossus. A single dorsal ganglionated root unites with this composite nerve. Thus the hypoglossus is a fusion of at least three segmental nerves, and the occipital region corresponds to as many vertebræ. (This view has been independently arrived at by McMurrich on purely anatomical grounds.) It must further be admitted that the occipital region of the cranium is not identical throughout the vertebrate series.

Ahlborn, from his studies on *Petromyzon* and *Anura*, has also arrived at the view that the hinder portion of the skull and the anterior cervical vertebræ may not respectively be homologous in different Craniates. He has come to the conclusion, mainly from a consideration of the cephalic mesodermic segments, that there were primitively nine pairs of spinal nerves in the hind-brain, of which Nerves III., IV., and VI., had only motor roots; but as neural segmentation (neuro-merism) is secondary, the spinal-like cerebral nerves of the craniota cannot be compared with the segmental spinal nerves.

An endeavour has been made to give a brief account of some of the views which are held respecting the significance of the cranial nerves, and of a few of the attempts which have been made to utilise the nerves in solving the problem of the segmentation of the Vertebrate head. It must, however, be borne in mind that there are very good reasons for regarding the apparent segmentation of the cephalic region as an arrangement perfectly distinct from the metamerisation of the trunk.

Sense Organs.—The simplest organs of sense are epiblastic cells, which, having a stiff hair-like process, are excited by vibrations in the external medium (fig. 119). These sense-cells are usually collected into groups or series, and constitute definite sense organs.

Sense organs may be roughly grouped into those which appreciate vibrations of air or matter, and those which are stimulated by light.

It is usually possible to distinguish between sense organs which have a tactile, olfactory, gustatory, and auditory function; but in the lower animals it is probable that other kinds of vibrations may be appreciable which give rise to sensations of a less distinct, or even of a different character. These various senses are doubtless differentiations of a primitive tactile sense; this is rendered more probable from the similarity in their development and their fundamental similarity of structure.

Tactile Organs.—Tactile organs are direct modifications of epidermal cells; they may either be the simplest of sense-cells, or

may be more or less differentiated. Numerous kinds of tactile organs are described in works on comparative anatomy and histology. They may be generally diffused or restricted to certain prolongations of the body, more especially of the anterior end, such as tentacles, palpi, and antennæ.

Olfactory Organs.—The higher invertebrate Metazoa alone possess any organs which can be recognised as olfactory. In the

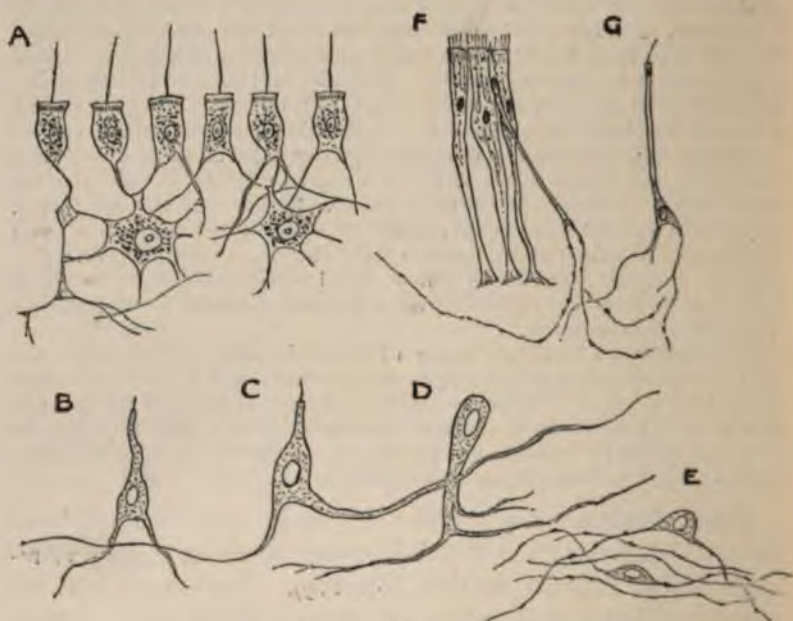


FIG. 119.—SENSE-CELLS OF CŒLENTERATES.

- A. Isolated sense-cells from dorsal nerve-ring in connection with two multipolar ganglion cells (from *Egginura myosura*). [After Haeckel.]
 B-E. Isolated elements from the upper nerve-ring of *Carmarina hastata*. [After O. and R. Hertwig.]
 B. Ordinary small sense-cell. C. Large sense-cell. D. Large ganglion cell. E. Ordinary ganglion cells and nerve-fibrills.
 F. Three supporting cells and one sense-cell from tentacle of *Anthea cereus*.
 G. Isolated sense-cell from the same. [After O. and R. Hertwig.]

Arthropoda these are minute bristles which are connected with nerve-fibrils. The olfactory organ of Mollusca (osphradium of Lankester) consists of a patch of sense-cells which is situated over each gill.

A pit or papilla behind or above each eye is stated to be the olfactory organ of the Cephalopoda.

In *Amphioxus* a single ciliated pit, situated on the left side at the anterior end of the neural canal, is usually spoken of as an

olfactory organ; but Hatschek has shown that it is of hypoblastic origin (p. 185).

An undoubted olfactory organ is present in all higher Chordata. It first appears as a pair of tracts of columnar epiblast at the anterior end of the body, immediately in front of the stomodæum (fig. 94, A, *olf*). The sensory epithelium invaginates as two shallow pits (fig. 117, 120), which soon deepen. Although the internal epithelium (Schneiderian membrane) is thrown into folds to increase the sensory surface, or the surface may be further increased by the projection of coiled, and sometimes very complicated, cartilages and bones (turbinal bones), yet the sac-like character and the primitive opening of the nasal pits are always retained.

The single nasal sac of the Cyclostomi has probably no phylo-

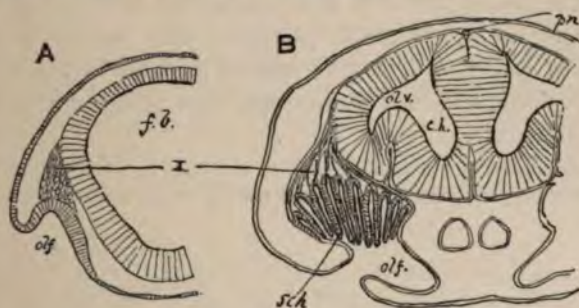


FIG. 120.—SECTIONS THROUGH TWO STAGES IN THE DEVELOPMENT OF THE OLFACTORY ORGAN OF AN EMBRYO DOG-FISH (*Scyllium*). [After A. M. Marshall.]

A. Early, B. Later stage.
c.h. cerebral hemisphere; f.b. fore-brain; olf. olfactory pit; ol.v. olfactory vesicle or lobe; p.n. pineal gland; sch. Schneiderian folds; i. olfactory nerve.

genetic significance, as in the younger stages there are distinct evidences of a double nature. In all other Vertebrates the nose is paired from the first.

In Elasmobranchs the orifice of the olfactory pit is ventrally situated. In the Ganoids and Teleosts a distinct and often wide bridge of tissue divides the orifice of the nasal sac into an afferent and an efferent orifice, which always come to be situated on the dorsal aspect of the snout.

A groove extends in many Elasmobranchs from each nasal sac to the mouth; the central flap of skin between the grooves is the nasal valve or fronto-nasal process (fig. 121). The lateral folds of the fronto-nasal process sometimes fuse with the cephalic integument across the nasal groove, in this way forming two apertures to the nasal sac.

The walls of this groove grow over and coalesce in the middle in Dipnoi and all higher animals, thus forming a canal which opens in front by the anterior nares or nostrils, and behind as the posterior nares. The latter are situated just behind the upper lip in Dipnoi and Urodela. In Anura and higher forms they lie somewhat farther back, but they are, in all, morphologically in



FIG. 121.—UNDER SURFACE OF HEAD OF DOG-FISH.

f, nasal flap, reflected on the left side of the fig. ; *g*, nasal groove ; *m*, mouth ; *na*, opening of olfactory organ.

front of the palatine bones. With the formation of the palate, the mouth cavity becomes subdivided into two, a lower buccal cavity and an upper nasal passage. The secondary posterior nares thus established may be carried back, as in the Crocodilia, Myrmecophaga, and in some Cetacea, even to the extreme hinder end of the mouth.

The development of the nasal passage in the Fowl is briefly as follows. The edge of the nasal pit develops a thickened border, except towards the mouth, thus



FIG. 122.—VENTRAL VIEWS OF THE HEADS OF EMBRYO FOWLS. (1) At the end of the fourth day of incubation. (2) At the commencement of the fifth day. [From Kolliker.]

an, outer nasal process ; *in*, inner nasal process ; *k'*, second visceral arch (hyoid) ; *m*, mouth ; *n*, nasal or olfactory pit ; *nf*, nasal groove ; *o*, superior, and *u*, inferior, maxillary process of the first (mandibular) visceral arch ; *x*, cavity of pharynx ; *sp*, choroidal fissure of the eye ; *st*, fronto-nasal process.

leaving a shallow groove, the nasal groove. The central portion of this groove is converted into a canal by the lower angle of the fronto-nasal process overlapping, and ultimately fusing, with the superior maxillary process. The nasal canal thus formed opens well within the mouth by the posterior nares.

The adult condition of the nasal groove in some Elasmobranchs (fig. 121) corresponds with a transient stage (fig. 122) in the embryos of those Vertebrates which have posterior nares.

The organ of Jacobson is primitively developed as a pair of diverticula from the nasal sac. These are at first large, but their subsequent development is less rapid than that of the olfactory sacs. Eventually they give rise to comparatively small organs, which usually open directly into the mouth independently of the posterior nares.

A shallow depression, which extends from the eye to the nasal pit while the nasal groove is still open, separating the outer nasal process (as the outer raised border of the nasal pit is termed) from the superior maxillary process, is known as the lachrymal groove.

The lachrymal duct is formed from a solid cord of epiblast cells which separates from the floor of the groove. It subsequently becomes hollow, and places the orbit in communication with the nasal chamber.

Gustatory Organs.—The gustatory organs always retain so simple a condition that they require no special mention.

Auditory Organs.—The so-called auditory organs of the invertebrate Metazoa are very varied in origin and position, but, except in the case of a few Medusæ, they are all epiblastic structures.

Some of these organs appear to possess a truly auditory function. Balfour has suggested that in some cases their function may be to enable the animals provided with them to detect the presence of other animals in their neighbourhood, through the undulatory movements in the water caused by the swimming of the latter. In the case of the Medusæ, however, the vibrations of waves reflected from the shore and rocks would affect these organs, and may possibly warn the Medusæ of danger.

Two forms of auditory organ are found amongst the Medusæ, the first alone being purely epiblastic, and consisting of an open sac, which may be converted into a complete cup. These occur along the base of the velum in the Vesiculate Hydromedusæ. Some of the cells form a concretion (otolith) within their walls, and others are sense-cells with auditory hairs, which lie close to the former (fig. 123, A, B).

The second form is found in the Trachymedusæ and Acraspeda, and consists of a modified tentacle, the terminal endodermal cells of which secrete otoliths, but the auditory hairs are solely ectodermal. The whole structure is usually more or less enclosed within a reduplication of the ectoderm, sometimes forming a vesicle which entirely surrounds the auditory tentacle. In all cases the auditory cells of the Medusæ are connected with the peripheral nerve-ring (fig. 123, *u.n.r.*).

Paired otocysts containing several otoliths, rarely one, occur in some Nemerteans, Nematodes, and a few Annelids. Practically nothing is known of their structure, and their origin is also unknown; this also applies to the unpaired otocyst of Planarians.

The otocysts of Mollusca develop as epiblastic pits (fig. 124) close to the proliferating areas which form the pedal ganglia. Very rarely they are at first solid. The pits are converted into rounded vesicles, from which a small ciliated canal (ductus Köllikeri)

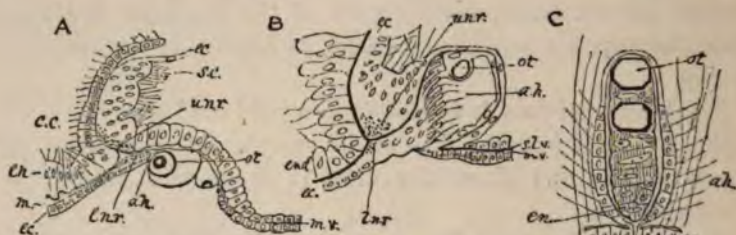


FIG. 123.—AUDITORY ORGANS OF VARIOUS MEDUSÆ. [After O. and R. Hertwig.]

A. Open auditory pit of *Mitrocoma annæ*. B. Closed auditory sac of *Equorea forskalea*. C. Endodermal otoliths in a modified tentacle of *Cunina lativentris*. a.h. auditory hairs; c.c. circular canal; ec. ectoderm; en. endoderm; l.n.r. lower nerve-ring; m. muscle-fibres; m.v. muscle of velum; ot. otolith; s.l.v. supporting lamina of velum; u.n.r. upper nerve-ring.

often projects, this being the remnant of the tube which for a time connects the vesicle with the orifice of the primitive invagination. At first a single small concretion is secreted by one of the cells of the vesicle; this may increase in size, and persist as a single otolith; in other cases it remains small, and a large number of minute concretions are added (*Pteropods*, *Dentalium*, *Nautilus*, most *Gastropods*). Rarely the numerous otoliths fuse to form a single large one

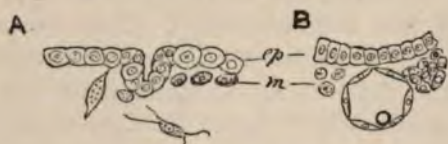


FIG. 124.—TWO STAGES IN THE DEVELOPMENT OF THE OTOCYST IN MUREX.

A. Open pit. B. Closed vesicle, with small otolith.
ep. epiblast; m. mesoblast.

(*Paludina*, *Decapods*). The interior of the vesicle is clothed with cilia; but in the specialised otocysts of *Heteropods* there is a patch of definite auditory cells (*macula acustica*), and a similar ridge (*crista acustica*) occurs in *Decapods*. The otocyst often shifts its position anteriorly, and usually comes to be innervated from the cephalic ganglion.

The *Arthropoda* never possess otocysts comparable with those of other Invertebrates. Unicellular hairs, or setæ on various parts

of the body, especially on the antennæ of Crustacea, are generally regarded as auditory; they are usually lodged within cuticular depressions.

In the Carididæ (Shrimps and Prawns) the auditory hairs usually occur on the basal joints of the antennules and on the tail; auditory pits may occur at both ends of the body. In the Schizopods a large otolith is present, which is secreted by the walls of the sac, and is renewed after moult. The auditory sac is situated in the caudal endopodite. The auditory hairs are restricted in Decapods to the basal joint of the antennules; they are usually feathered, and often bent. The otocyst in these forms may be widely open (Palinurus), but the opening is usually reduced to a narrow fissure. In Hippolyte the sac is completely closed. Only in the Crabs does the otocyst become

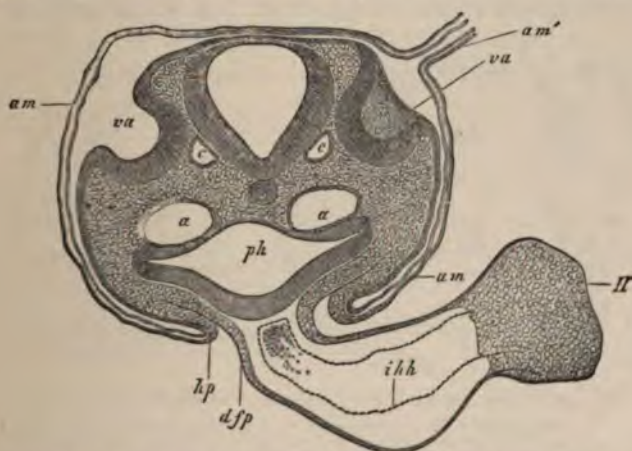


FIG. 125.—TRANSVERSE SECTION THROUGH THE AUDITORY INVOLUTIONS OF AN EMBRYO FOWL OF THE SECOND HALF OF THE SECOND DAY. Magnified 24 diameters. [From Kölliker.]

a. descending aortæ; am, amnion, with its two layers; am*, amniotic suture, situated on the right side and not drawn in its whole extent; c. root of the inferior cerebral vein; dip, splanchnic mesoblast (fibro-intestinal layer) of the pharynx, continuous with the external envelope of the heart and forming an inferior cardiac mesentery; H, heart; hp, somatopleur passing into the amnion; ihh, endothelium of the heart; ph, pharynx; va, widely open auditory sac.

at all complicated. The otoliths are entirely foreign particles, and appear to be introduced by the animal itself.

A remarkable sense organ, usually stated to be acoustic, is found in certain Hexapoda, and is situated either on the thorax or at the base of the legs. It consists essentially of a series of nerve-fibres, each of which passes into a nerve-cell, from which arises a multicellular elongated structure, usually containing a stiff rod. The multicellular fibre is usually attached to a tympanum, supported by a chitinous ring. The whole structure is always situated over an air sac.

In Appendicularia there is a single otocyst on the left side of the ganglion, consisting of a spherical sac enclosing a spherical otolith which is supported by delicate isolated hairs. In other pelagic Tunicates there are two symmetrically placed otocysts; their development is not known. In fixed Ascidians an otolith is developed from a single cell on the dorsal and right side of the brain. This cell projects into the cavity of the brain, and its free end is pigmented. Eventually the cell becomes

stalked, and travels round the right side of the brain until it reaches the summit of a patch of cylindrical sense-cells, the crista acustica. The adult organ thus consists of a crista acustica on the floor of the anterior region of the brain and projecting into its cavity, upon which is perched an oval otolith, the lower part of which is clear and refractive, while the upper half is pigmented. This is the only known example of a cerebral auditory organ.*

The Organs of the Lateral Line.—In Teleostei the sense organs of the lateral line appear in segmental patches of simple sense-cells; each area is then invaginated to form a short groove, which partially closes over. The fusion of these channels forms the canal of the lateral line, but numerous external openings are left. The lateral line of Elasmobranchs is at first a solid cord of cells,

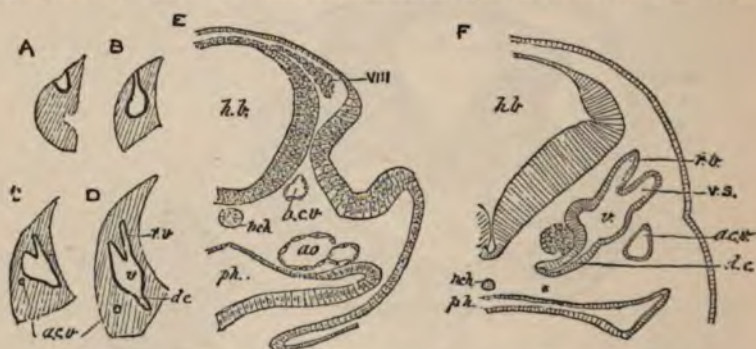


FIG. 126.—EARLY STAGES IN THE DEVELOPMENT OF THE VERTEBRATE EAR.

A-D. Four stages in the development of the labyrinth of a Powl. [After Reissner.] E. Transverse section through the auditory pit of a Fowl's embryo of fifty hours. [After Marshall.] F. Transverse section through the head of a foetal Sheep (16 mm. in length) in the region of the hind-brain. [After Böttcher.]

a.c.v. anterior cardinal (jugular) vein; a.m. amnion; a.o. aortic arch; c.g. cochlear ganglion; d.c. ductus cochlearis; h.b. hind-brain; h.c. notochord; ph. pharynx; r.v. recessus (aqueductus) vestibuli; v. vestibulum; v.s. vertical semicircular canal; viii. auditory nerve.

but this is probably an abbreviated process. In Chimæra the lateral line persists in the adult as an open groove. (See also p. 139.)

The Vertebrate Ear.—The auditory organ of Vertebrates may possibly prove to be a highly specialised organ of the lateral line series. The auditory sac first appears as a shallow depression of the epiblast in the region of the posterior brain vesicle above the first (hyoid) visceral cleft (figs. 125, 126). It soon becomes a flask-shaped vesicle which is separated from the skin, although in some Elasmobranchs the primitive opening to the exterior is retained throughout life.

The stalk of invagination persists as the aqueductus vestibuli, and its blind swollen distal extremity is the saccus endo-lymphaticus or recessus vestibuli (figs. 126 and 127, r.v.).

The swollen portion of the primary auditory vesicle is modified

to form the utriculus and the semicircular canals, while a ventral diverticulum gives rise to the cochlea and the sacculus hemisphericus.

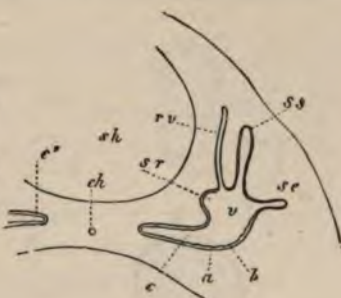
The rudiments of the anterior and posterior semicircular canals grow out from the lateral wall of the vesicle as two flattened processes. Their central walls become applied together, obliterating the cavity, except at the circumference, and eventually the centre is absorbed, leaving two ring-like canals. The horizontal semicircular canal is developed somewhat later in a similar manner.

The Cylostomi possess two imperfect vertical canals, which, with the utriculus, form a ring-shaped membranous labyrinth. All other Vertebrates have the three semicircular canals.

The body of the primitive vesicle persists as the vestibule or utriculus.

FIG. 127.—TRANSVERSE SECTION OF AUDITORY LABYRINTH OF AN EMBRYO COW, $2\frac{1}{2}$ lines in length. Magnified 30 diameters. [From Kölliker.]

a. boundary of the cavity in the cranial wall containing the epithelial labyrinth (b), which does not everywhere fill up the cavity; c. mouth of cochlea; c'. lagena of cochlea; ch. notochord; rv. recessus vestibuli; sc. horizontal (external) semicircular canal; sh. cranial cavity; sr. mouth of sacculus hemisphericus (?); ss. vertical semicircular canal; v. vestibulum.



The cochlea of Mammals higher than the Monotremes consists of a helicoid spiral tube, connected with the utriculus by a narrow canalis reuniens. It develops as a simple process from the inferior end of the auditory vesicle. The various stages in its development in the higher forms are permanently retained in the adults of various lower animals.

The sacculus hemisphericus is a round vesicle which is evaginated from the base of the cochlea shortly after the appearance of the horizontal canal. A constriction opposite the mouth of the aqueductus causes the passage between the utriculus and the sacculus to diverge slightly up the aqueductus instead of pursuing a straight course (fig. 128).

The simple epiblastic aural invagination becomes in this manner a complicated labyrinth. The sense-cells are restricted to certain tracts, and, with the exception of the organ of Corti, they retain a very simple character. The auditory hairs project into the fluid (endolymph) contained within the labyrinth. The otoliths or

otoconia are masses of carbonate of lime secreted by the lining epithelium.

The neighbouring mesoblast enters into relation with the auditory apparatus, the cells immediately surrounding the labyrinth being converted into a connective tissue investment (the membranous labyrinth). The whole being protected by a cartilaginous, and, in most animals, a subsequently osseous capsule, which is known as the osseous labyrinth. The latter is undeveloped at one spot, the fenestra ovalis in Elasmobranchs, Amphibia, and higher animals. A second foramen occurs in Mammalia, the fenestra rotunda.

Between the membranous and osseous labyrinths imperfect lymph spaces are found in the Sauropsida; these are well developed in the Mammalia.

In the cochlea of the latter two longitudinal lymph-spaces are formed, the dorsal of

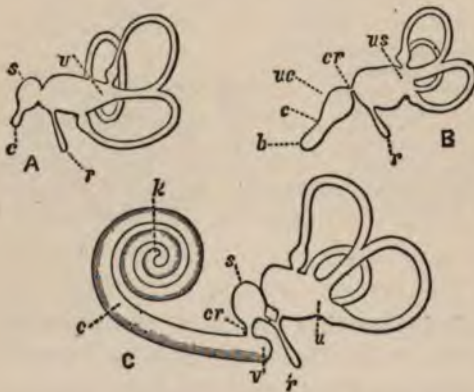


FIG. 128.—DIAGRAM OF THE AUDITORY LABYRINTH: A. of a Fish; B. of a Bird; C. of a Mammal. [From Bell after Waldeyer.]

b. lagena; c. cochlea; cr. canalis reuniens; k. coil (helix) of the cochlea; r. recessus vestibuli; s. sacculus; u. utriculus or vestibulum with the three semicircular canals; v. caecal sac.

which (scala vestibuli) communicates with the cavity round the membranous labyrinth, and at the apex of the cochlea is continuous with the ventral space (scala tympani). The latter terminates blindly at the fenestra rotunda. The fluid contained within these lymph spaces is the perilymph.

It must not be forgotten that the cavity (scala media or canalis cochleæ) lying between the two scalæ is the sensory portion of the cochlea, and is alone lined by epiblast. The scalæ and the bony labyrinth are protective structures.

In most Fish the labyrinth or internal ear is more or less enclosed within the ear capsule, and is quite cut off from the outer world, the sound vibrations passing through the skull to the ear. But in some Teleosts the fenestra ovalis or its equivalent is in connection with the air-bladder through the intervention of a chain of ossicles (*e.g.*, Cyprinoids and Siluroids). (See p. 181.)

Howes calls attention to a fenestra in the roof of the chondrocranium of many Elasmobranchs situated behind the orifice of the aqueductus vestibuli, the covering of which evidently functions as a tympanic membrane.

The hypoblastic diverticulum of the pharynx, which forms the hyoid cleft of Fishes (see p. 178), may acquire an external opening

in some Amphibia which soon closes over. In all higher Vertebrates it persists as a blind recess, the Eustachian tube, dilating distally into a chamber (tympanic cavity) which partially surrounds the utriculus.

The external auditory meatus corresponds to the lower section of the outer or epiblastic portion of the original hyoid cleft. The meatus is formed principally, if not entirely, by the growth of the surrounding tissue in such a manner as to leave a deep tube. A pit (Hunt's depression), corresponding to the upper section of the cleft, soon disappears. The external ear, concha or auricle, appears early (in the Pig) as a small triangular flap arising from the anterior border of the hyoid arch opposite the meatus; it corresponds in position with the operculum of Fishes.

The tympanum in Mammals is at first a vertical thick wall of tissue separating the Eustachian tube from the shallow external depression, much as in Amphibia. By the subsequent extension of the two tubes the tympanum is reduced to a thin membrane, and is situated in a plane perpendicular (instead of parallel) to the surface of the head. The outer epithelium of the tympanum is clearly of epiblastic origin, while the inner epithelium is hypoblastic.

There is in Amphibia and Sauropsida a bony rod, the columella auris, extending from the fenestra ovalis to the tympanum. The greater portion, according to Parker, is a dismembered section of the hyoid arch; the base (stapes) being a plug of cartilage severed from the auditory capsule.

A chain of three ossicles, the stapes, incus and malleus, connects the tympanum with the fenestra ovalis in Mammals; the first of these is homologous with the Reptilian stapes, but there has been a good deal of discussion concerning the nature of the last two bones. Huxley and Parker's original view was, that the incus is the proximal portion of the hyoid arch and the malleus is the arrested quadrate; the processus gracilis of the malleus representing the primitive continuation into Meckel's cartilage. The current view in Germany is that both the incus and the malleus belong to the mandibular arch (in which case the former might represent the quadrate and the latter the articular element of the lower jaw). This homology, which was independently arrived at by Salensky and Fraser, now receives Parker's unqualified support. According to Reichert, the stapes is part of the hyoid arch, but Salensky and Fraser hold that it arises from a mesoblastic blastema which surrounds the mandibular artery, hence the perforation of the stapes.

Albrecht maintains, however, that the quadrate cannot form part of the chain of auditory ossicles of Mammalia, and that the zygomatic portion of the squamosal is the homologue of the quadrate of Sauropsida. Dollo supports this conclusion, and adds that he has found an element in Lacertilia which he homologises with the malleus of Mammalia. He slightly modifies Albrecht's series of homologies in the following

manner. The symplectic + hyomandibular of Teleosts or the suspensorium of Fishes generally equals the columella of Urodeles and the four ossicles of Anura. These, again, are equivalent to the malleus + columella of Sauropsida and the malleus + incus + os lenticulare + stapes of Mammalia.

Visual Organs.—The more or less definite appreciation of those vibrations of ether which result in the sensation of sight is a faculty which is readily acquired by the outer cells of the body, hence what are termed eyes have appeared perfectly independently in numerous groups of the animal kingdom. Even in the same order of animals eyes of quite dissimilar morphological value may occur, as, for example, the eyes in the shells of certain Chitons [Moseley], on the back of Onchidium [Semper], on the edge of the mantle, and on the siphon of numerous Lamellibranchs; but it is almost certain that the cephalic eyes of the Odontophora, when present, including even the transient eyes of larval Chitons, are homologous all through the group.

It is probable that the power of distinguishing light from darkness is a primary characteristic of protoplasm; if this be so, it would necessarily be readily retained by epiblastic cells, especially if pigment is present. Semper has suggested that a simple rounded tubercle covered with a transparent cuticle, or a mere local thickening of the cuticle, would serve to concentrate rays of radiant energy and would stimulate the adjacent cells; but eyes appear to have been derived from the much more elementary condition of a small patch of pigmented epithelium. From such a simple beginning almost any kind of eye can be derived without special difficulty.

Eyes of Invertebrates.—Eyes consisting of but slightly modified epithelial cells covered by a thickened cuticle occur in nearly all the lower Metazoa. It is characteristic of the eyes of the Invertebrates that the light falls directly on the sensory (retinal) cells, their inferior extremities being connected with nerve-fibrils which transmit the stimulus to the nerve centres. The dorsal eyes of Onchidium and the pallial eyes of Pecten and Spondylus offer a remarkable exception to this rule, as in these Molluscs the rays of light, after passing through the cornea and lens, have to penetrate a layer of nerve-fibres before impinging upon the sense-cells. Patten has shown that in Pecten this is due to the primitive optic cup being converted into a vesicle, of which the lower (inner) wall becomes aborted, the retina being formed of the upper (outer) wall. The sensory surface of the latter would necessarily be internal to

the cup, and the nerve layer external. The same general arrangement also occurs in the eye of the Chordata.

The simplest eyes in the Arthropoda are those of the larvæ of certain Insects; in these the hypodermis forms a slight depression (fig. 129), the lowermost cells of which form the retina, and are connected with the fibres of the optic nerve; a biconvex thickening of the cuticle forms the lens.

Lankester, working on the lines of Grenacher, has suggested the following stages of evolution as occurring in the Arthropod eye:—

Instead of remaining distinct (non-retinulate), the retinal cells may be aggregated together to form what is termed a retinula, as in the lateral eyes of Scorpions and *Limulus*, and the eyes of Myriapoda.

A higher stage of differentiation consists in the division of the retinal cells into an outer vitreous and an inner retinal layer. These double-layered eyes (diplostichous, as opposed to the above-mentioned single-layered or monostichous eyes) may either be composed of separate cells (non-retinulate), as in the dorsal eyes of Spiders and the simple eyes of adult Insects, or the sensory cells may be grouped into retinulae.

The retinulate diplostichous eyes may either be provided with a single lens

FIG. 129.—SECTION OF EYE OF LARVA OF A WATER-BEETLE (*Dytiscus*). [From Bell after Grenacher.]

An example of a non-retinulate, monostichous, monomeniscus eye.

g-p. optic cup; *h.* hypodermis (epidermis); *l.* lens; *o.* optic nerve; *r.* retina.



(monomeniscous), as in the central eyes of Scorpions and *Limulus*, or the cornea may become divided into a number of lenses or facets (polymeniscous), as in the compound eye of Insects and Crustacea.

It seems that a non-retinulate eye cannot be polymeniscous, since the segregation of retinulae is the developmental antecedent of the segregation of the lens. Hence we may have monostichous polymeniscous eyes (lateral eyes of *Limulus*) as well as diplostichous polymeniscous eyes, but all non-retinulate eyes are monomeniscous. The compound (polymeniscous) eye is formed, not by the gradual concrescence of a number of simple eyes, but by the segregation of the elements of a simple eye, which affects first the retina and then the lens.

All these structures are modifications of the epiblast.

It is stated that in *Astacus* the corneal lenses and the crystalline cones are directly developed from the epiblast of the optic pit which very early makes its appearance on the procephalic lobes of the embryo; while the retinulae with their rhabdoms, together with the optic ganglion and nerve, are developed from the cephalic ganglion. But, it will be remembered, the latter also arises from a proliferation of the epiblast of the same area. The pigment is stated to be derived from neighbouring mesoblast cells, but the visual pigment is probably epiblastic.

Patten believes the development of the Decapod eye to be as follows:—The cephalic epithelium (hypodermis) gives rise, by cell proliferation, to two layers—an inner one, the brain; and an outer one, the permanent epidermis. That part of the brain arising from the seat of the future eye gives rise to the optic ganglion, which is never entirely

separated from the seat of its origin. That part of the epidermis from which the optic ganglion originated again thickens and divides into two layers, an outer corneal hypodermis and an inner ommateal layer, consisting of retinophoræ surrounded by their circles of retinulæ (see p. 156).

Kingsley has very recently found that in Crangon, the cephalic pits, which Reichenbach formerly believed to be concerned in the development of the cephalic ganglia,

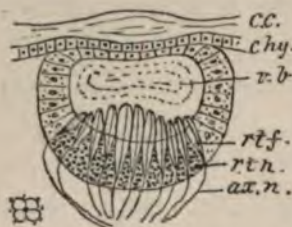


FIG. 130.—OCCELLUS OF LARVAL INSECT. [After Patten.]

ax.n. axial nerve; c.c. corneal cuticle; c.hy. corneal epidermis (hypodermis); rt.f. retinophore. Each retinophore (retinal cell of Grenacher) consists of a group of four cells round an axial nerve. The cuticular portion or rod of each retinophore is provided with a plexus of nerve-fibrils (not shown in fig.), and projects into the optic vesicle; rta. retinulæ or pigmented cells; v.b. vitreous body.

A section of a retinophore showing the peripheral and axial nerves is placed by the side of the figure.

are the rudiments of the eyes. Each optic pit is converted into a vesicle which sinks below the epidermis. The outer portion of the optic vesicle develops into the retina, while the inner portion forms the ganglionic layer. Later mesoblastic cells migrate between the retina and the ganglionic layer; these subsequently become pigmented. Nerves grow from the ganglionic layers into the retinal elements. The eyes are only connected with the cephalic ganglia at about the time of hatching.

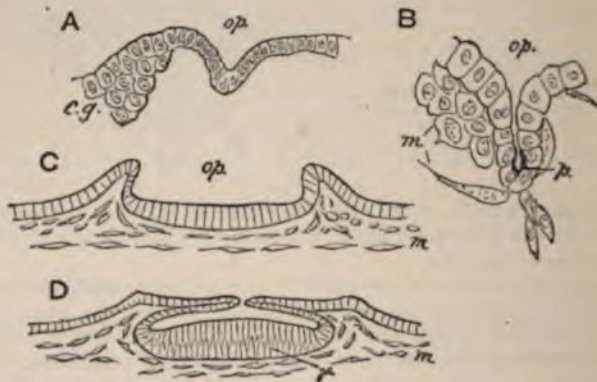


FIG. 131.—SECTIONS THROUGH THE DEVELOPING EYES OF MOLLUSCS.

A-B. Gasteropod (*Murex*). C-D. Cephalopod (*Loligo*). [The latter after *Lankester*.]

c.g. proliferation to form cephalic ganglion; m. mesoblast; op. optic pit; p. pigment; r. retina.

According to Patten, the primitive optic pit (fig. 129) is converted into an optic vesicle (fig. 130), the anterior wall of which atrophies, while the posterior is greatly thickened to form the retina. This view differs fundamentally from Grenacher's.

The cephalic eyes of the Mollusca arise as a single pit of the epiblast from the area from which the cephalic ganglia proliferate, and at the base of the tentacles (fig. 131, A).

Fraisse first demonstrated that the eyes of the Limpet (*Patella*) never advance beyond this stage of development (fig. 132), and that *Haliotis* is intermediate between this larval eye and the eyes of such Gasteropods as *Fissurella* (fig. 132, c) or *Helix* (fig. 133, B).

In the last two forms, as in most other Odontophora, the embryonic pit is converted into a vesicle, the inner wall of which constitutes the retina. The lens is a cuticular deposit. The outer wall of the vesicle, together with the overlying epidermis, form the cornea. The eyes of *Chætopoda* and *Peripatus* are very similar to this.

The stalked eyes of the *Nautilus* (fig. 133, A) always persist as

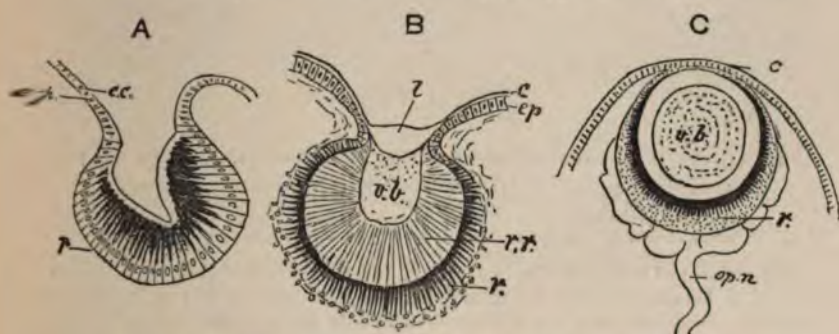


FIG. 132.—DIAGRAMS ILLUSTRATING THREE STAGES IN THE EVOLUTION OF EYE OF GASTEROPODS. [A and C. after Fraisse; B. after Patten.] A. *Patella*. B. *Haliotis*. C. *Fissurella*.

In A. the eye persists as a simple optic cup. In B. the lower or reticulate layer of the cuticle is converted into the retinal rods; the corneal layer is divided into a semi-fluid inner portion (*v.b.*) and a harder outer portion (*l.*). In C. the optic cup is converted into a vesicle, and the epidermis is continued under the cornea.

c. cornea; c.c. corneal cuticula; ep. epidermis; l. lens; ep.n. optic nerve; r. retina; r.r. rods of retinophore; v.b. vitreous body.

a simple optic pit, although considerable differentiation occurs in the retinal cells.

The most complex type of eye occurring amongst the Invertebrata is found in the Dibranchiate Cephalopoda. In these forms the two stages just mentioned are passed through, but a second smaller lens is secreted by the corneal epiblast immediately in front of the former, and an annular pigmented fold of skin (fig. 133) which develops round the front of the eyeball functions as an iris. Later a circular fold surrounds the eye; it may either grow completely over, or leave a smaller or larger central aperture. This fold becomes transparent and forms a secondary cornea; the space between it and the lens is known as the anterior optic chamber. An eyelid is usually superadded. The secondary cornea passes below into a tough mesoblastic sheath or "sclerotic," which is further protected externally by a cartilaginous capsule. The optic cavity is bounded behind by the several layered retina, and in front by the lens; a ciliary body is developed where the retina joins the lens. The outer wall of the eyeball contained within the anterior optic chamber is sometimes termed the choroid.

The complexity of this type of eye is merely the result of secondary folds of the external skin (iris, cornea, eyelid), more or less enclosing the typical Molluscan eye. The white body is a problematical structure which is situated at the side of the optic ganglion (see p. 114). Although the eye of these Cephalopoda strangely simulates that of Vertebrates, there is a profound morphological dissimilarity, which is readily apparent when their development is compared together.

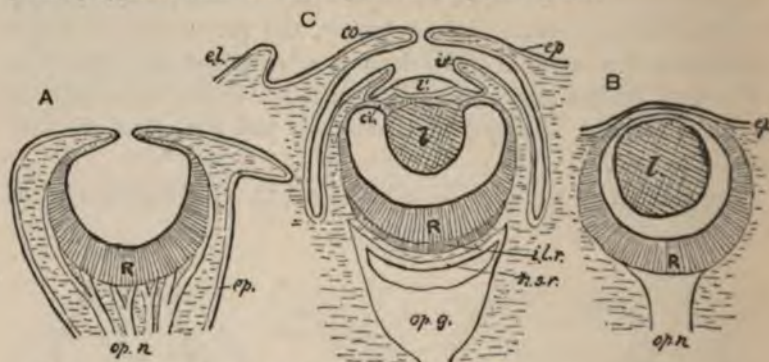


FIG. 133.—THREE DIAGRAMMATIC SECTIONS OF THE EYES OF MOLLUSCA. [After Grenacher.]

A. Nautilus. B. Gasteropod (*Limax* or *Helix*). C. Dibranchiate Cephalopod.
 el, epithelium of ciliary body; co, cornea; el, eyelid; ep, epidermis; i.l.r., inner layer of retina; ir, iris; l, lens; l', outer segment of lens; n.s.r., nervous stratum of retina; op.g, optic ganglion; op.n, optic nerve; R, retina.

The nature and evolution of eyes of certain Invertebrates has most recently been studied by Patten; his views briefly are that the structural element (ommatidium) of all eyes consists of from two to four colourless cells (retinophoræ) surrounded by a circle of pigmented ones (retinulæ). The external cuticle consists of two layers, an outer structureless one (corneal cuticle), and an inner layer (retinidial cuticle),

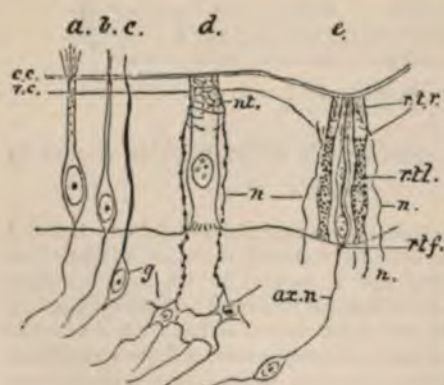


FIG. 134.—DIAGRAM REPRESENTING THE TRANSFORMATION OF EPIDERMAL CELLS INTO SENSE- AND NERVE-CELLS IN MOLLUSCA. [After Patten.]

a, neuro-epithelial cell with its nervous prolongation, transformed in c to a bipolar and in d to a multipolar nerve-cell (g); d, a myo-epithelial cell with its radiating fibres forming a basal membrane, two hypodermic nerves (n) are shown, the fibrils of which form a network (nt, retia terminalia) on the upper portion of the cell and in the lower layer of the cornea; at e the essential portion (ommatidium) of an invaginate eye is figured: the central retinophora (rtf) is composed of two cells, whose nuclei persist, enclosing an axial nerve (ax.n) which supplies its retinal rod; the two lateral pigment cells, retinulæ (rta), have also retinal rods (rta), which, however, disappear in more specialised eyes; their nerves (n) form a network on the rods; c.c., corneal cuticle; r.c., retinidial cuticle.

filled with the retia terminalia or ultimate ramifications of the hypodermic nerves. The cuticular secretion of each cell forms a rod containing a specialised part of the retia terminalia (retinidium).

In the more specialised ommatidia the rods of the retinulæ disappear, leaving the double (ex. Molluscs, Worms) (fig. 134) or quadruple (crystalline cone of Arthropoda) (fig. 130) rods of the retinophoræ.

The apposed walls of the retinophoræ disappear to a greater or less extent, so that the nerve-fibres between the cells come to lie in the centre of the group, and constitute the axial nerve (fig. 134, *ax.n.*).

According to Patten, the epidermis of Molluscs consists mainly of columnar cells, the inferior expansions of which form the basal membrane. The cuticle secreted by these cells consists of two layers, an outer corneal layer (fig. 134, *c.c.*) and an inner retinidial layer (*r.c.*). The nerve-fibres of the skin ramify into an extremely delicate fibrillar network on the upper portion of these cells, and into the lower (retinidial) layer of their corresponding cuticular areas or rods (fig. 134, *n.t.*). An eye is initiated by the appearance of (red) pigment in one or more of these cells, the red pigment (ommerythrine) being peculiarly sensitive to light vibrations. An optic element or ommatidium consists of a group of such pigmented cells (retinulæ) round one or more colourless nervous cells (retinophoræ). Although at first all the cells of an ommatidium are sensitive, the retinophoræ persists as the truly sensitive cells, while the retinulæ take on secondary functions. It must be distinctly understood that Patten alone is responsible for the above conclusions.

Lankester draws attention to the fact that "it is difficult to make out what precisely is the situation and the limit of the pigment in all Arthropod eyes." Pigment granules are often very freely developed in the protoplasm of the ordinary hypodermis (epidermis) cells and of the indifferent cells (both perineural and interneural) of the ommateum. Should the nerve-end cells be pigmented, the pigment granules are confined to the surface of the cell, leaving the axis transparent.

"The relation of pigment to the optical apparatus cannot be said to be at present properly understood. It is perfectly certain that in some eyes, and possibly in all, pigment does not play a primary part in the physiological process set going by light. Light acts with full effect upon transparent protoplasm, and no pigment is necessary, converting the energy of light into the energy of heat, in order that the protoplasm of cells may constitute an apparatus sensitive to light. The function of pigment in an eye is a secondary one, as we learn from the sight of albino varieties. What precisely the significance of pigment may be in relation to the cells in which the optic nerve ends, is not yet agreed upon by physiologists."

Eyes of Vertebrates.—The eyes of the Vertebrata are of a compound nature, part being developed from the brain and part from the outer skin of the head; both these elements are therefore of epiblastic origin, and they are protected by mesodermal structures.

The first rudiment of the eye to appear is a pair of diverticula, which bud out from the sides of the anterior cerebral vesicle (figs. 106, *abl.*, and 110, *mes.*), and which are known as the primary, optic vesicles. They usually arise as soon as the primitive brain shows traces of serial dilatations (cerebral vesicles); but in some Mammals, at all events, the optic vesicles are recognisable before the cerebral neural groove is converted into a canal.

The optic vesicles at first have a wide opening into the brain, but they are soon partially constricted off, and their narrowing stalks will develop into the optic nerve. The constriction which separates the optic vesicle from the brain extends from above and from the front, so that the stalk of the vesicle is situated at the

base of the brain, and arises from the posterior region (thalamencephalon) of the anterior cerebral vesicle.

The external wall of the optic vesicle invaginates until it is completely inverted (fig. 135), recalling the manner in which a blastula is typically converted into a gastrula.

The epiblast of the head, which lies immediately external to the optic vesicles, becomes columnar, and invaginates as a rounded vesicle at the same time that the optic vesicle is introverted. The sac thus formed is the rudiment of the lens (fig. 112). As this becomes constricted off, the outer skin again becomes continuous, and is eventually transformed into the cornea.

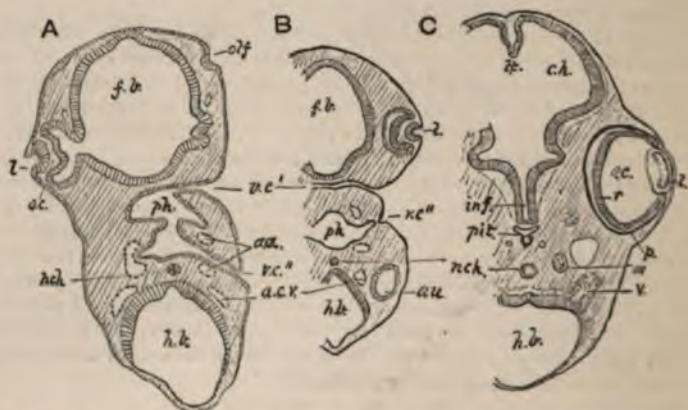


FIG. 135.—HORIZONTAL SECTION THROUGH THE HEAD OF AN EMBRYO FOWL, ILLUSTRATING THE DEVELOPMENT OF THE EYE.

A. Embryo of fifty-four hours' incubation. [After Marshall.] The section is oblique; on one side it passes through the optic stalk.

B. Section of about the same age, through another plane. C. Later stage.

a.a. aortic arches; a.c.v. anterior cardinal (jugular) vein; au. auditory vesicle; c.h. cerebral hemispheres; f.b. fore-brain; h.b. hind-brain; inf. infundibulum; l. lens; l.t. lamina terminalis; nch. notochord; o.c. optic cup; p. pigment layer of the retina; ph. pharynx; pit. pituitary body; r. retina; v.c. visceral clefts.

The eye at this stage consists of a stalked double-layered cup, containing a hollow sphere, and bounded externally by the skin (figs. 112, 135A). The cavity within which the lens lies is known as the secondary optic vesicle, or, more correctly, as the optic cup. The lens does not grow so rapidly as the optic cup, and consequently is soon relatively much smaller, and comes to be embraced by the rim of the mouth of the cup (figs. 135, C, 136).

The various elements of the eye will now be described separately, but previously certain points concerning the mode of the invagination of the optic vesicle require consideration.

The invagination does not occur solely on the outer face of the

optic vesicle, but also, in a linear manner, along its ventral line. The cup thus has a wide mouth, plugged by the rudiment of the lens, and a ventral slit (choroidal fissure) which opens into the cavity of the eyeball (fig. 136, *ch.f.*).

To again borrow a simile, the orifice of invagination of the optic cup may be said to resemble a linear blastopore with an anterior enlargement. The latter persists, but the former ultimately becomes closed.

It is at present an open question how far the invagination to form the optic cup is primitively the result of the pressure of the lens.

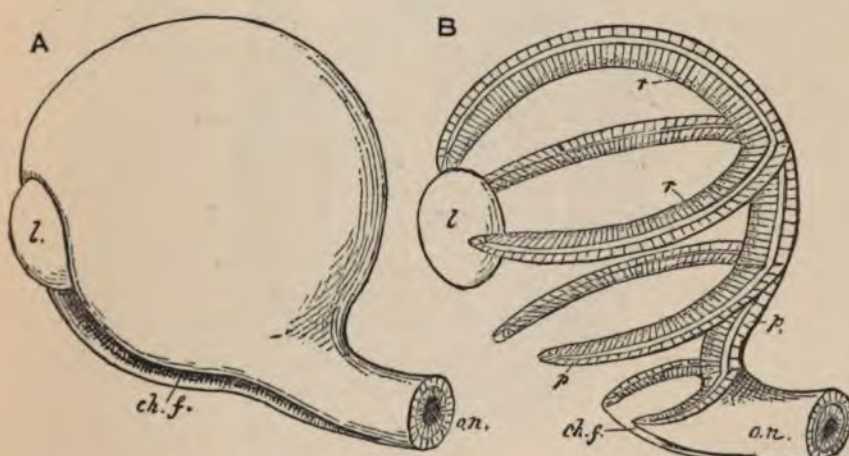


FIG. 136.—DIAGRAM ILLUSTRATING THE POSITION OF THE CHOROIDAL FISSURE.

A. Surface view, from the side. B. Skeletal view, the greater portion of the optic cup being supposed to be cut away.

ch.f. choroidal fissure; *L.* lens; *a.n.* optic nerve; *p.* pigment layer; *r.* retina.

From the first, the inner or anterior layer of the optic cup is thicker than the outer or posterior, and it becomes increasingly so. The former is the rudiment of the retina, while the latter persists as the pigment layer within which the retinal rods are imbedded (the so-called pigmented epithelium of the choroid) (figs. 137, *p.ch.*; 138, *p.*).

The retina soon becomes several cells deep, but it is probable that for some time, at least, each cell extends throughout its whole thickness. The histogenesis of the retina is still obscure. It however appears to be unquestionable that the layer of rods and cones is developed from the epithelial layer of the central nervous system (fig. 139); and that the main portion of the retina, with its nerve-

fibres and nuclear layers, together with the inner (anterior) layer of nerve-fibres and nerve-cells, is formed from the more specially nervous portion of the cerebral epiblast.

The optic nerve is, as has already been stated, derived from the stalk of evagination of the optic vesicle. The reduction of the cavity of the canal by the thickening of its internal walls takes place centripetally, *i.e.*, from the eye to the brain.

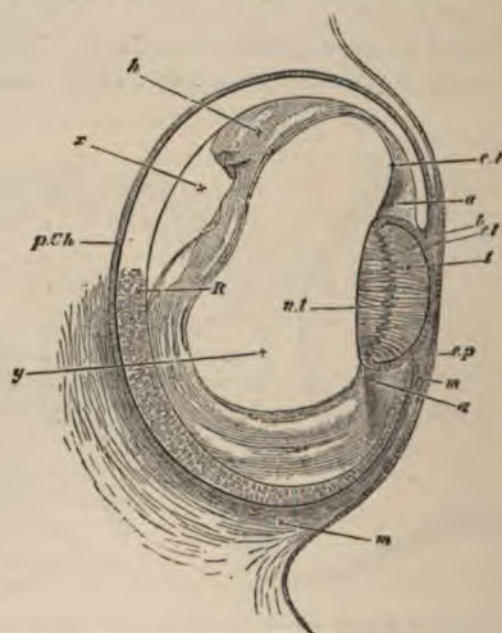


FIG. 137.—SECTION OF THE EYE OF A FOWL AT THE FOURTH DAY.
[From Balfour.]

s.p. superficial epiblast of the side of the head; *R*, true retina, anterior wall of the optic cup; *p.Ch.* pigment epithelium of the choroid, posterior wall of the optic cup; *b*, is placed at the extreme lip of the optic cup, at what will become the margin of the iris; *l*, lens,—the hind-wall, the nuclei of whose elongated cells are shown at *n.t.*, now forms nearly the whole mass of the lens, the front wall being reduced to a layer of flattened cells, *e.f.*; *m*, the mesoblast surrounding the optic cup, and about to form the choroid and sclerotic,—it is seen to pass forward between the lip of the optic cup and the superficial epiblast.

Filling up a large part of the hollow of the optic cup is seen a hyaline mass, the rudiment of the hyaloid membrane and of the coagulum of the vitreous humour (*v*). In the neighbourhood of the lens it seems to be continuous, as at *e.f.*, with the tissue *s*, which appears to be the rudiment of the capsule of the lens and suspensory ligament.

While the optic stalk is still partially open, fibres appear in its proximal portion, some of which pass over into the root of the other, and thus initiate the optic chiasma. The nerve-fibres later extend along the optic stalk.

The optic nerve is at first continuous with both layers of the optic cup (fig. 136), but in process of time the connection with the outer or pigment layer is lost.

In Mammals the distal portion of the optic stalk is flattened and its cavity obliterated whilst the optic cup is forming; and since the stalk itself partakes in the invagination, the choroidal fissure may be said to extend for some distance along the nerve. The central blood-vessels of the retina (fig. 138) enter this groove, and are subsequently surrounded by the overgrowth of the nerve. The retinal circulation is entirely confined to these vessels and their capillaries. Kölliker suggests that the invagination of the optic stalk is due to the pressure of the mesoblast, which develops into the blood-vessels.

The retina is unprovided with true retinal blood-vessels in animals lower than the

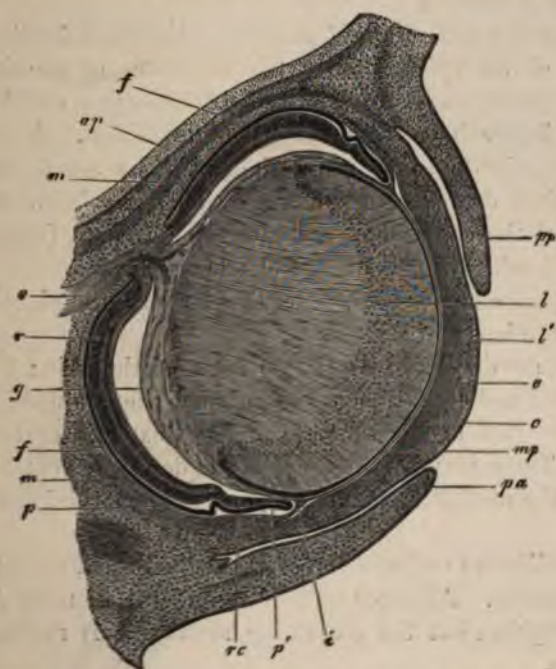


FIG. 138.—HORIZONTAL SECTION OF THE EYE OF A RABBIT OF EIGHTEEN DAYS. Magnified 30 diameters. [From Kölliker.]

ap. orbito-sphenoid (lesser wings of the sphenoid); *c.* cornea, with its anterior epithelium; *e.* rudiment of the choroid; *g.* vitreous body detached from the retina by shrinkage, except behind, where the central artery of the retina passes into it; *l.* iris; *l'* crystalline lens; *f.* epithelium on the anterior face of the lens; *m.* rectus superior, and *r.* inferior muscles; *mp.* membrana pupillaris; *o.* optic nerve; *p.* outer pigmented layer of the retina; *p'* anterior border of secondary optic cup, where the retina proper passes into the pigmented layer; *pa.* upper eyelid; *pp.* lower eyelid; *r.* retina; *rc.* pars ciliaris retinae.

Mammals, but their place is possibly to some extent taken by the vascular structures which penetrate the cavity of the eyeball through the choroidal fissure. These are known as the *processus falciformis* in Ichthyopsida, and the *pecten* in Sauropsida.

The lens was left as an oval vesicle, with uniformly thick walls. Very soon the cells of the front wall become thinner and flattened, while those of the inner wall elongate and entirely obliterate the cavity of the vesicle (fig. 137). The latter cells early become

strap-shaped and acquire their final disposition (fig. 138). At no time is the wall of the lens more than one cell deep.

The lens capsule is a cuticular membrane probably secreted by the epithelial cells of the lens.

The vitreous humour appears to be derived from a fluid transudation from the vascular ingrowth, which enters the retinal chamber through the choroidal fissure. In some cases a few embryonic mesoblast cells occur.

The anterior epithelium of the cornea is formed by the growing together of the epiblast after the formation of the lens. Its deeper or proper substance is of mesoblastic origin, and is derived from an ingrowth of the neighbouring mesoblast. A similar but shorter inferior fold constitutes the iris. The mesoblast cells of the incipient cornea occupy a space which lies between the epithelium of the cornea and a flattened epithelium (membrane of Descemet), which is also of mesoblastic origin.

The aqueous humour is a watery fluid which occupies the cavity between the lens and the cornea.

Eyelids are developed as simple folds of the skin; their inner surface is lined by a mucous membrane, the conjunctiva, which also covers part of the sclerotic and the exposed surface of the cornea. There may be three eyelids, a dorsal, a ventral, and an anterior, the nictitating membrane, arising from the inner angle of the eye.

The eyelids are rudimentary or absent in Fishes, except in some Elasmobranchs. All three eyelids are present in most Amphibia and Sauropsida, but the nictitating membrane is rudimentary in Mammals.

In many Mammals the two eyelids meet together and unite during a period of embryonic life. A similar condition is permanent throughout life in Snakes and some Lizards, the lachrymal ducts opening into the space thus formed between the fused lids and the cornea.

Lachrymal glands occur in the Amniota. Their character varies greatly in the different groups, but they always arise as solid ingrowths of the conjunctiva.

The sclerotic and choroid coats of the eye are protective envelopes developed from the mesoblast.

Epiphysial Eye.—The possession of a rudimentary median eye, lodged in the parietal foramen and developed from the pineal gland, in several Lizards has already been alluded to (p. 129). The lens

of this eye is a direct derivative of the optic cup, and what light reaches it impinges directly on the retina without first penetrating through the retinal layer of the fibres of the optic nerve (fig. 138*, D). Thus, as in the Pectinidæ and Onchidium, certain Invertebrates have accessory eyes constructed on the vertebrate plan, so some Lacertilia amongst the Vertebrates possess a typically invertebrate unpaired eye. A radical distinction between the pineal eye of Lizards and the eyes of Invertebrates consists in the fact that the essential constituents (retina and lens) of the former

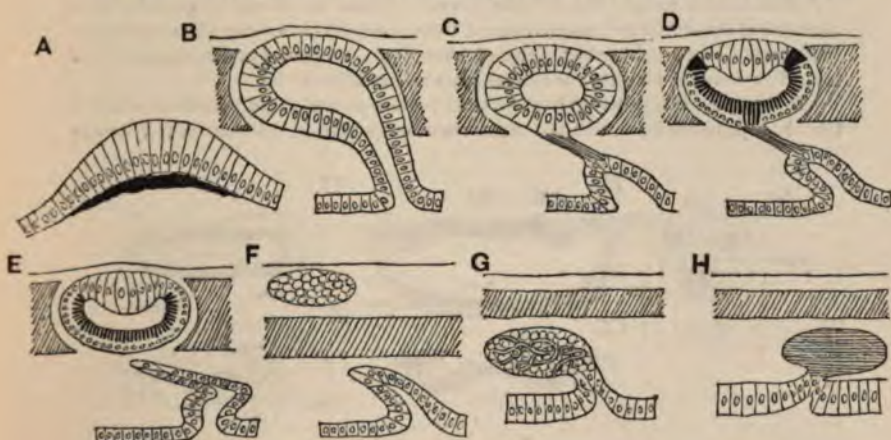


FIG. 138*.—DIAGRAMS ILLUSTRATING THE EVOLUTION OF THE EPIPHYSIS (Pineal Gland). [After Spencer.]

A. Early stage of epiphysis in *Bufo cinerea*; this corresponds with the early stage in larval Tunicates and the probable condition in the ancestral Chordate. B. Early stage in all higher Chordata; permanent in Elasmobranchs and Cyclopus. C. Later stage in Anura and Sauropsida; permanent in Chameleo. D. Adult stage in certain living Lacertilia, e.g., *Hatteria*, *Varanus*; probable condition in Labyrinthodonta, and in ancestors of Reptilia and Aves. Final stage in many Lacertilia, e.g., *Calotes*, *Seps*, *Lelodera*. F. Anura, adult. G. Aves, adult. H. Mammalia, adult. It will be seen from the above figure that the epiphysal or pineal eye of certain living Lizards is differentiated from the distal vesicular portion of the pineal gland. The central section being converted into an optic nerve, the proximal practically forms an optic lobe. A-D, illustrate the development of the organ to its most specialised condition. E-H, indicate various phases of degeneration. The shaded portion indicates the parietal bone. In D, the anterior portion of the vesicle is modified to form a lens, the posterior wall differentiating into an inner pigmented retinal layer and an outer layer of nerve-cells.

are entirely differentiated from a diverticulum of the brain (fig. 138*, C-E), whereas in the latter they are invariably epidermal structures.

Hypothetical Evolution of the Vertebrate Eye.—The fact that the optic cup is developed from the anterior brain vesicle is at first sight very anomalous. The following considerations, however, may tend to throw some light upon it.

It will be remembered that an ancestral form of the Chordata was assumed (p. 76) to possess a nervous system but little differentiated from the epiblast extending along the primitive oral aspect of the body, and expanding in front of the mouth. Upon this region a pair of cuplike eyes was supposed to be situated, the eyes having

essentially the same structure as in *Patella* (fig. 132). This condition is diagrammatically represented in fig. 139, A, B, the latter being a supposed transverse section through the pre-oral region of A. It will be seen that the eye-pits are connected with the pre-oral neural epiblast, much in the same manner as the eye-pits of Mollusca (fig. 131) are developed in connection with the proliferations which form the cephalic ganglia (fig. 96, c, g).

The involution of the nervous area to form the neural canal also implicated the optic pits (fig. 139, C). Since this figure was drawn, Heape has shown that in the Mole the optic vesicles appear as depressions of the cephalic neural plate even before the neural groove is established. Heape figures a section which very closely resembles the diagram given in C, fig. 139. On the closure of the neural tube the pits would appear as vesicles (optic vesicles) opening into the anterior cephalic enlargement.

A local thickening of the overlying lateral epiblast to form a lens might be a mechanical cause for the invagination of the optic vesicle to form the optic or retinal cup. Every subsequent stage of evolution, being an optical improvement, could be accounted for once the retinal cup was established.

Fig. 139 also illustrates that the visual sense-cells (rods and cones) are derived from the epithelial layer of the central nervous system, in other words, from the

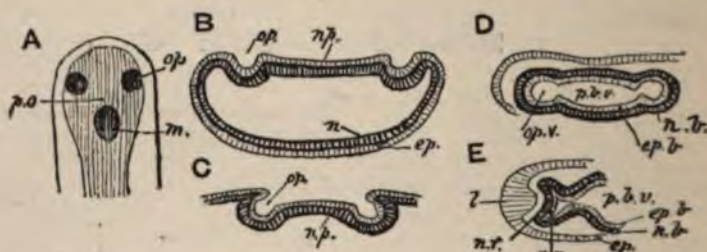


FIG. 139.—DIAGRAMS ILLUSTRATING A HYPOTHETICAL EVOLUTION OF THE VERTEBRATE EYE.

A. Surface view of head of a hypothetical type. B. Vertical section of same across the optic pits. C. Invagination of the pre-oral neural plate and optic pits. D. The process completed. E. Formation of lens and optic cup.
ep. epidermal layer of epiblast of head; ep.b. epithelium of brain; l. lens; m. mouth; n. nervous layer of epiblast of head; n.b. nervous layer of brain; n.p. neural plate; n.r. nervous layer of retina; op. optic pit; op.v. optic vesicle; p.b.v. primary brain vesicle; p.o. pre-oral neural plate; r.r. layer of rods of retina.

external epiblastic epithelium; that is to say, from precisely the same layer which gives rise to the similar elements in Invertebrates. The deeper or nervous layer of the epiblast is concerned in the formation of the layer of nerve-fibres and nerve-cells of the retina.

The transparency of the body of the primitive Chordata, assumed by Lankester, would enable light to reach the optic pits, although the latter were situated within the brain. But as the animal became more opaque, it may be assumed that the visual apparatus (optic vesicles) would grow out towards the sides of the head through which most light would penetrate. The lens is clearly a secondary structure. On this hypothesis the eye could be functional whilst it was undergoing this unique metamorphosis.

Observations on the Evolution of the Nervous System and Sense Organs.—

The origin of the nervous system and sense organs from the epiblast is one of the best attested of embryological discoveries, and from the foregoing brief account they would appear to be universally so derived. The only general statement, however, that can be made is that nerve and sense cells have arisen in response to a stimulus, or, more correctly, as the result of a stimulus.

As a matter of fact, such a stimulus would most readily and frequently act upon

the exterior of the body, and therefore upon epiblastic tissue; hence the almost universal origin of these structures from that layer; but there are a few exceptions which are of considerable interest.

The brothers Hertwig have demonstrated that in addition to the diffused ectodermal nervous system present in the Actiniae, there is a distinct layer of nerve fibres and cells, and in some cases of sense-cells, which can only be derived from the endoderm. The occurrence of the latter may possibly receive an explanation from the fact that the mesenteric chambers open widely into the digestive cavity of the body in these animals. As the wide mouth and oesophagus are so generally open, there is really considerable facility for stimuli, such as vibrations in the external medium, to act upon the internal tissues. In both cases, therefore, the differentiation occurs in tissues directly exposed to the surrounding medium.

Quite recently Hubrecht has discovered that the nervous system, *i.e.*, the brain and lateral nerve cords of the Nemertean Worm *Lineus obscurus* are derived from the mesenchyme. Certain of these wandering cells (mesamœboids) apply themselves to the interior of the body-wall in definite areas, and there differentiate into the nervous system of the adult. The mesenchyme has a double origin, being partly derived from the epiblast and partly from the hypoblast (fig. 49). Although direct proof is not attainable, it is fair to assume that the nervous system is developed out of the epiblastic rather than from the hypoblastic mesenchyme. If this be the case, it is probably another example of "precocious segregation."

As has been already mentioned (p. 114), Bobretzky states that the nervous system of the Prosobranch Gasteropod *Fusus* is derived from the mesoblast, and that the wandering cells apply themselves to certain areas of the epiblast, as in the case of *Lineus*, but in all the other Gasteropods which have been examined, and even in the allied forms of *Purpura* (fig. 96) and *Murex*, the nerve centres have an epiblastic origin. Bobretzky's statement must therefore be received with caution. The same applies to Fol's account of the origin of the pedal ganglia from the mesoblast of the foot of *Limax*, while the cephalic ganglia are developed from the epiblast of the velum.

Lastly, the origin of the sense-cells and nerve-cells of Sponges, which have been described by Stewart, Von Lendenfeld, and Sollas, is still somewhat uncertain. They have been stated to be mesodermal (mesenchyme) elements, from the fact that the ectoderm of Sponges always occurs as a delicate flattened epithelium and never exhibits any transitional stages into sense-cells, in this respect offering a marked contrast to that of Coelenterates. Whereas the position and appearance of the nerve and sense-cells irresistibly suggest a mesodermal origin.

One important point should not be lost sight of in these considerations. It is that protoplasm from its very nature is what has been termed "irritable," that is to say, it responds to stimuli. This irritability is inherent to all cells, and probably is never lost while the cell lives; certain cells have this function greatly developed, while in others it is more or less diminished. It is probable that stimuli may readily pass from one cell to another in most tissues, as animal cells are usually in close contiguity when not in actual continuity. In many adult animals, and usually in embryos, different tissues may be connected together by branched mesoblastic cells (indifferent connective tissue), which may also be amœboid. If these latter cells retain their irritability, there is probably nothing to prevent their transmitting as well as receiving stimuli. They may thus serve as incipient nerve-fibres; and it is further possible that this function may be sufficiently pronounced to cause the formation of a definite nervous tissue which is purely mesoblastic in origin. This secondary nervous system might be developed in adults as well as in embryos. The observations of Von Lendenfeld on Sponges tend to support this hypothesis.

From numerous researches on the nervous system of the lower Metazoa, it is not difficult to trace the stages by which ectodermic (epiblastic) cells are gradually modified into nerve-cells.

In the primitive Metazoon most of the external cells of the body were probably ciliated, and had very similar functions. In process of time certain cells would gradually acquire a greater degree of sensitiveness, while others would become more protective in function. If, for instance, a cilium-like prolongation of a cell lost its power of contractility and became rigid, it would then, as a mechanical necessity, vibrate in response to the vibrations of the surrounding medium. These induced vibrations would act as stimuli to the cell and excite a manifestation of irritability, which might expend itself in various ways. Most sense-cells are constructed on this plan; they are, in fact, epidermal cells with a stiff projecting hair or rod-like process, and are inferiorly continuous with other cells.

Chatin has recently found that all intermediate stages can be found between the auditory rods and ciliated cells of the auditory epithelium of the labyrinth in Batrachia.

It is now demonstrated that the cells of the tissues of the Coelenterata are connected with each other by means of very delicate, usually branching, root-like processes, which serve for the contraction and general co-ordination of the parts or whole of the organism or colony. The sense-cells form no exception, and in some of them the upper sensory portion appears to be gradually becoming smaller, while the lower portion, which contains the nucleus, is swollen (fig. 119, c, e). As the nucleus is mainly the centre of the activity of the cell, it may be assumed that in these cells general irritability is preponderating over special sensibility, and that it only needs a slight further specialisation to constitute a cell wholly given over to irritability; in other words, a nerve-cell. The same process also occurs in the skin of Molluscs. In fig. 134, a, b, c, d, diagrammatically represent the gradual transformation of a sense-cell, a, into a multipolar nerve-cell, g.

The nerve-cell retains connection with the neighbouring cells by its root-like processes, and thus may be united with a sense-cell on the one hand, and with a glandular or muscular cell on the other. By this double connection the nerve-cell may receive a stimulus from a sense-cell, and by the excitation of its own irritability may transmit the stimulus in an intensified form to the distal cell, and the latter will be stimulated to perform its special function.

The foundation of a distinct nervous system will thus be laid, and the multiplication and localisation of sense-cells and nerve-cells has probably been effected to a large extent independently in the different groups.

This suggestion concerning the evolution of the nervous system seems to be warranted from a consideration of the histology of adult Coelenterates (fig. 119) and Molluscs (fig. 134); but even if it be a correct interpretation of the facts in these groups, it is possible that in other forms the history may be somewhat different. For example, nerve-cells may originate by the division of certain epidermal cells into an outer protective portion and an inner more irritable or nervous moiety, the latter always retaining connection with the former by means of protoplasmic threads.

In the embryos of the lower Chordata the epiblast primitively consists of a single layer; in *Amphioxus* alone is this condition retained in the adult. In the *Urodele* Amphibia the epiblast is single layered till the completion of the gastrula stage; but in the *Anura* the epiblast is several layers thick in the blastula stage.

In all cases the distinctly nervous elements of the central nervous system and sense organs is formed entirely from the deeper layer of the epiblast. Thus there is in the *Anura* and some other groups, Ganoids and Teleosts, an early separation of the epiblast into the epithelial and the mucous or nervous layer.

Spencer has recently stated that the segmental nerves and ganglia in the Frog arise *in situ* by a local persistence of this deeper layer; thus there is, as he points out, in Amphibia a primitive nervous sheath to the body, the nervous tracts being local retentions of this diffused nervous system. Later still Misses Johnson and

Sheldon, from their studies on the Newt and Frog, support the generally received view of the outgrowth of the nerves from the neural ridge.

In this connection it is interesting to notice that Bateson has shown that in *Balanoglossus* (the lowest known member of the Chordate series) the central nervous system arises as a delamination of a solid cord of epiblast in the dorsal middle line of the middle third of the body of the embryo; this, by invagination of its two ends, is afterwards extended as a tube in both directions. Other collections of nerve-fibres are afterwards deposited in various parts of the body, and finally a general network of nerve-fibres occurs on the under surface of the skin of the body, especially in the line of the gill-slits. The tail-like processes of the epiblast cells run into the different superficial nervous tissue, and many fibres pass into the subjacent mesoblastic tissues. The fibres entering this nerve-substance on its outer side are plainly sensory, or at all events afferent, and the fibres passing from it on its inner side are presumably motor, or at least efferent, seeing that they innervate the mesoblast.

"It is clear, then (as Bateson points out), that on the separation from the skin of a cord thus composed the relations of the efferent fibres will not be changed, as they still remain in contact with the mesoblast. But, on the other hand, if this nerve-cord be entirely separated from the skin, the supply of outer or afferent fibres is cut off from it, unless cords of epiblast remain to connect it with the skin. Applying this reasoning to the particular case of the separation of the dorsal cord, we see that the afferent fibres are entering it on its dorsal side, and that the efferent fibres are leaving it on its ventral side. If the nervous system arose in this way, the dorsal roots were from the first sensory, and did not arise as differentiations of roots of mixed function, as has often been supposed."

The epithelium lining the cavity of the central nervous system and the sensory epithelium of the sense organs are derived from, or from what corresponds to, the external layer of the epiblast. Exceptions occur in the auditory sacs of Ganoids and Teleosts, which are solely developed from the deeper layer of the epiblast, and in the optic vesicles of Teleosts, which are formed as solid buds from the solid nervous keel which will develop into the brain. In this, as in many other respects, the development of the Teleosts is extremely modified.

CHAPTER VI.

ORGANS DERIVED FROM THE HYPOBLAST.

IN a previous section the archenteron was left as a simple sac or tube, opening to the exterior anteriorly by the stomodæum, and posteriorly by the proctodæum.

From what was said concerning the effects of the presence of a large amount of food-yolk, it will be obvious that there will be a discrepancy in the relative time of the development of various hypoblastic structures; for example, in telolecithal ova the ventral wall of a considerable portion of the alimentary canal must of necessity be completed very late.

The primitive function of the hypoblast is undoubtedly alimentation, but in the course of evolution it has acquired several other functions. The digestive organs will now be first considered, and subsequently other hypoblastic derivatives will be described.

Digestive Organs.—The simple sac-like archenteron of the gastrula, as has already been described, is produced into pouches in a large number of animals.

When this occurs in Sponges the characteristic hypoblast cells (choano-flagellate cells) become restricted to the extremities (ciliated chambers) of the often complicated diverticula. All the exhalent canals are lined with flattened hypoblast cells.

The gastric diverticula of Cœlenterates appear to be chiefly concerned with the circulation or distribution of the nutritive fluid, the actual process of digestion being probably confined to the stomach of the Hydromedusæ, and the edges of the mesenteries in the Actinozoa (fig. 68).

In the Cœlomata, or those animals provided with a true body cavity, these diverticula are cut off from the gastric cavity, and are henceforth spoken of as mesodermal structures.

The gastric diverticula of the Turbellarians, of certain Nemer-teans, and of the Leeches, cannot be regarded as coelomic diverticula which have never severed their connection with the archenteron.

It has been shown (p. 29) that in most centrolecithal ova (*e.g.*, Crustacea) some of the hypoblast cells engulf the food-yolk which lies within the segmentation-cavity (fig. 22). In other ova the yolk is originally located within the primitive hypoblast. In both cases it is digested by those cells.

The actual conversion of the primitive hypoblast into special digestive cells has not been fully investigated, but it must be readily effected, as digestion and assimilation are primary properties of protoplasm.

The hypoblastic portion (mesenteron) of the alimentary canal is always divisible into definite regions, and, with the exception of most of the Arthropoda, it forms by far the largest section of the tract.

The various regions of the alimentary canal of different animals which appear to be similar had received corresponding names before their development was known, consequently many apparent morphological anomalies must be expected.

Usually among the Invertebrates the stomodæum is prolonged as the œsophagus; the mesenteron includes the stomach and intestine and their associated glands, while the proctodæum is small. The Arthropoda, as a whole, are an exception to this rule, for in Insects the mesenteron is that portion of the alimentary canal lying between the crop or proventriculus, when that is present, and the point of origin of the Malpighian tubes. The mesenteron may be a simple tube, or divided into regions, of which the anterior may possess numerous small cæca (some Beetles) or eight large ones (Cockroach). In low forms, such as the Myriapoda and Peripatus, the mesenteron is long and simple.

In the lower Crustacea the mesenteron is relatively long. There are in Amphipods, in addition to the two or four digestive cæca, which are so commonly present throughout the Crustacea, two long narrow tubes which open into the extreme hinder end of the mesenteron. These tubes are undoubtedly excretory, but, as Spencer has shown, they are hypoblastic and not epiblastic, they cannot be regarded as homologous with the Malpighian tubules of the Tracheata (p. 111).

The mesenteron of the Decapod Crustacea is restricted to the usually minute chamber between the so-called pyloric chamber (fig. 140) and the commencement of the intestine (proctodæum); it is separated from the former by valves. It is to this that the term stomach should be restricted. The digestive gland or so-

CHAPTER VI.

ORGANS DERIVED FROM THE HYPOBLAST.

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The primitive function of the hypoblast is undoubted, but in the course of evolution it has acquired several new functions. The digestive organs will now be first considered, and subsequently other hypoblastic derivatives will be described.

Digestive Organs.—The simple sac-like archenteron, or gastrula, as has already been described, is produced in a large number of animals.

When this occurs in Sponges the characteristic hypoblastic cells (choano-flagellate cells) become restricted to the extremities of the canals (chambers) of the often complicated diverticula. All the canals are lined with flattened hypoblast cells.

The gastric diverticula of Cœlenterates appear to be chiefly concerned with the circulation or distribution of the nutritive fluid, the actual process of digestion being probably confined to the stomach of the Hydromedusæ, and the edges of the mesenteries in Actinozoa (fig. 68).

In the Cœlomata, or those animals provided with a true body cavity, these diverticula are cut off from the gastric cavity, and are henceforth spoken of as mesodermal structures.

The gastric diverticula of the Turbellarians, of certain Nemertean worms, and of the Leeches, cannot be regarded as cœlomic diverticula which have never severed their connection with the archenteron.

as it does, the function of liver and pancreas, it has been appropriately termed the hepato-pancreas. It is a complex gland which typically develops from the wall of the mesenteron (fig. 140) in the usual manner, but, in some forms, the liver appears to be formed by a metamorphosis of the remnant of the yolk-cells which remain after the formation of the mesenteron (fig. 84, B, *y*).

Mesenteron of Chordata.—The hypoblastic portion of the alimentary canal of the Chordata is divisible into the following regions: pharynx, cesophagus, stomach, and intestine (figs. 141, 143).

The egg being yolkless in *Amphioxus*, the archenteron (fig. 57) is directly converted into the alimentary canal of the adult.

The effect on the formation of the mesenteron by the presence

FIG. 141.—ISOLATED ALIMENTARY CANAL OF EMBRYO DOG OF TWENTY-FIVE DAYS. Multiplied 5 diameters. [From K lliker after Bischoff.]

a. pharyngeal or branchial pouches; *b.* rudiment of laryngeal portion of the pharynx; *c.* lungs; *d.* stomach; *f.* liver; *g.* dorsal wall of the vitelline sac, with which the intestine still communicates by a large orifice (the umbilicus); *h.* rectum.

The inner white line indicates the hypoblast; the surrounding dark border representing the splanchnic or visceral (mesoblastic) sheath of the alimentary tract. Compare with A, fig. 143.



at first of a small, and then of a gradually increasing amount of food-yolk, has already been described (p. 30). The constriction off of the digestive tract from the yolk-sac in telolecithal ova takes a comparatively long time, and not a few Fish are hatched with the yolk-sac still depending from their bodies. In fig. 141, which illustrates the isolated alimentary canal of an embryo Dog, viewed from the ventral surface, it will be seen that all the main organs have made their appearance while the umbilicus is still widely open (see also fig. 143). The neck of the yolk-sac gradually narrows to form the vitelline duct, and the first fold of the intestine (figs. 144, 1; 143, *c*) occurs at the spot where the vitelline duct joins it. A diverticulum which occasionally occurs in Man in the lower part of the ileum is the persistent b
vitelline duct;
vitelline duct

may persist in Birds as a short tube connected with the small intestine.

Pharynx.—The pharynx probably extended along a considerable length of the body in the primitive Chordata, as is still the case in *Amphioxus* and Lampreys. The lateral walls were devoted to respiratory purposes, as will be described subsequently.

A deep ciliated groove, the endostyle, extends along the median ventral line of the pharynx (branchial sac) in Ascidians. The cilia work from before backwards and thus carry the mucus, which is secreted by the glandular cells of the endostyle, along with entangled food particles into the œsophagus.

The hypopharyngeal ridge of *Amphioxus*, with its glandular cells, has a similar function.

This region corresponds to the non-respiratory ventral portion of the pharynx of *Balanoglossus*.

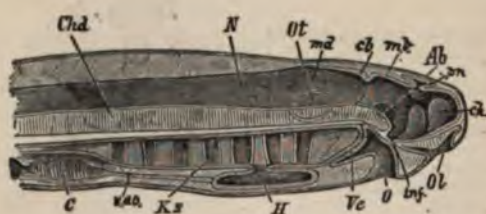


FIG. 142.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE HEAD OF A LARVAL LAMPREY (*Petromyzon*). [From Claus after Balfour.]

Ab, optic vesicle; C, heart; c2, cerebellum; c2, cerebral hemisphere; Chd, notochord; H, hypopharynx (thyroid involution); inf, infundibulum; Ks, branchial pouches; m2, mid-brain; m2, medulla; N, nervous system; O, stomodæum; Ol, olfactory pit; ot, auditory vesicle, represented as visible; pn, pineal gland (below which the optic thalamus is shown); v.2, ventral aorta; v, velum. The oblique line between the velum and the first branchial pouch represents the left of a pair of ciliated grooves which converge on the median ventral line to meet the orifice of the thyroid.

A considerable groove is developed in the front portion of the floor of the pharynx in the larval Lamprey (fig. 142), and to a decreasing extent in higher forms.

We may therefore conclude that the ventral portion of the primitive pharynx was concerned in the transmission of food. The special mechanism by which this was effected afterwards degraded into the median element of the gland known as the thyroid body (see p. 183). It is possible that this change of function was correlated with the increase in size of the primitive Chordata and the consequent ability to eat larger prey. The latter, from their size, would not have the tendency to escape through the gill-slits, which minute organisms could easily do, and would further pass into the œsophagus without requiring the assistance of the ventral groove. The latter, owing to disuse, would naturally degenerate.

Throughout the Ichthyopsida the pharynx gradually becomes greatly shortened, as is also the case in Amphibia and Amniota.

œsophagus.—The œsophagus calls for no special mention. It is a simple tube of variable length, which in some forms (*Crocodylia* and many Birds) has a ventral saccular dilatation or crop.

Stomach.—The œsophagus may pass imperceptibly or abruptly into the stomach. The stomach is usually a simple dilatation of the alimentary canal (figs. 141–144). Its exact form varies considerably, but it only becomes at all complicated in a few Mammals (*e.g.*, Sloths, Cetacea, Ruminants, some Marsupials and Rodents).

There is an instructive modification in the stomach of Ruminants during growth. In the early foetus the relative size of the compartments and general form of the stomach are almost exactly those of the adult. After birth, owing to the milk-diet, the growth of the peptic stomach or abomasus is greatly in excess of that of the others; but as a herbivorous diet is acquired, the characteristic form of the adult stomach is re-acquired.

To secure increase of secreting surface without proportionate extent of superficies, crypts or pockets of digestive cells were developed forming simple glands. In time these became more complex, as was previously described for epiblastic glands (p. 106), the cells which actually secrete the digestive fluid being restricted to the blind extremities or alveoli of the gland.

Three types of such glands are found in Mammals; the simple tubular crypts of Lieberkühn in the small intestine. A gland with a non-glandular duct and a few simple tubules is illustrated by the peptic and pyloric glands of the stomach, and the glands of Brunner in the pylorus, while the liver and pancreas represent the most specialised form of gland.

Liver.—The “liver” in *Amphioxus*, alone of all Chordata, retains its primitive tubular form. It is the earliest hypoblastic gland to be developed, and it is relatively very large in foetal life. It appears to be entirely absent in *Balanoglossus*.

In some of the lower Vertebrata (Elasmobranchs and Amphibia) (fig. 99) the liver arises from a single ventral diverticulum from the intestine, which soon becomes bilobed. In Birds and Mammals (fig. 141) the liver appears to be bilobed from the first.

The incipient liver buds out into a local thickening of the splanchnic mesoblast, which thus becomes penetrated by a number of rod-like prolongations (hepatic cylinders) of the primitive diverticula. As a rule the hepatic cylinders appear to be solid, but in Elasmobranchs Balfour found that they are hollow, as they are also stated to be in Amphibia. A system of ducts appears in due course. The hepatic cylinders have the peculiarity, which is unique among glands, of uniting with one another at numerous points, thus forming a network within the meshes of which the enveloping mesoblast develops into blood-vessels.

The gall-bladder is simply an enlargement of, or a diverticulum from, the main duct of the liver. Its presence is very variable;

the number and position of the ducts of the liver opening into the intestine are also inconstant in various animals.

Pancreas.—The pancreas occurs very constantly among the Vertebrates. It is absent in the Cyclostomi and Perennibranchiate Amphibia, and rudimentary or absent in many Teleosts. The pancreas may be partially imbedded in the liver in Ganoids, and completely so in Siluroids. It first appears as a tubular outgrowth from the dorsal wall of the intestine, opposite to, but slightly behind, the diverticulum, which forms the rudiment of the liver. According to His, the pancreatic rudiment at first appears in front



FIG. 143.—FOUR STAGES IN THE DEVELOPMENT OF THE HUMAN ALIMENTARY CANAL, AS SEEN FROM THE LEFT SIDE AND ISOLATED. [After His.]

all, stalk of allantois; b.p. bursa pelvis; c. caecum; ep. epiglottis; g.e. genital eminence; k. kidney; l. liver; la. larynx; l.d. duct of liver; lg. lung; l.j. lower jaw; p. pancreas; pr. proctodaeum; R.p. Rathke's pouch (hypophysial evagination, behind it in A and B is Seeke's pouch; st. stomach; t. tongue; th.p. median rudiment of thymus gland; tr. trachea; u. ureter; umb. umbilical vesicle; v.d. vitelline duct; W.d. Wolffian duct.

of the liver in the human embryo, and later shifts its position to behind that viscus (fig. 143, B-D). Hollow diverticula arise from the main duct, which continually subdivide. The surrounding mesoblast develops as usual into blood-vessels and connective tissue. In some cases two pancreatic diverticula have been observed.

Intestine.—The intestine is the post-gastric portion of the mesenteron. It is always a straight tube in embryos, and persists as such in many of the lower Chordata. In other forms it becomes variously looped, owing to its length exceeding that of the body cavity within which it lies.

The posterior portion of the intestine in the adult, but not in the embryo, is usually of markedly greater diameter than the anterior portion or small intestine; it is known as the large intestine.

The secreting and absorbing surface of the alimentary canal is increased in the lowest Vertebrates by the development of a longitudinal fold projecting into the cavity of the intestine, which is known as the spiral valve.

The fold is slightly developed in the Cyclostomi, and reaches its highest state of development in some Elasmobranchs. It becomes less marked in the Ganoids, and traces of it may be found in the intestine of a few Teleosts. In no higher Vertebrate has it been definitely recognised. A similar fold is found in the intestine of some Ascidians; such a fold may be compared with the typhlosole of certain Invertebrates (ex. Earthworm and Fresh-water Mussel).

FIG. 144.—ROUGH DIAGRAMS ILLUSTRATING THE CHANGE IN RELATIVE POSITION UNDERGONE BY THE DIGESTIVE TRACT IN MAMMALS. [From Landois and Stirling.]

c, colon; o, vitelline duct; r, rectum; t, small intestine; v, stomach.



Concomitantly, according to Wiedersheim, with the disappearance of the spiral valve in Fishes a number of hollow diverticula (pyloric caeca) make their appearance from the anterior region of the small intestine (duodenum). These are found in some Ganoids, in which group their development is not always inversely proportional to that of the spiral valve, and in most Teleosts, but in no other animals. Their function appears to be, in some forms, to increase the absorbing surface of the intestine, as a digestive function may be present or absent [Stirling, Macallum]. In a few Teleosts they occur side by side with the pancreas.

Those animals which possess a spiral valve have, in the main, an alimentary canal which pursues a straight course through the body cavity. In other forms (excepting Teleosts) the greater length of the intestine probably renders a spiral valve superfluous.

The relative length of the alimentary canal is largely dependent

upon the nature of the food of the animal. This is well illustrated in the case of the Frog's tadpole. When still subsisting upon its stored-up food-yolk, the alimentary tract retains its primitive straight course (figs. 98, 99). After the tadpole is hatched it commences to feed upon decaying vegetable matter, and the intestine grows to a great length, and is coiled up like a watch-spring. Later on the young Frog takes to an animal diet, and the intestine is relatively very much shorter, and is only slightly looped.

The valvulæ conniventes of Man, and similar folds in other animals, also serve to increase the absorbing surface of the small intestine. The development of all these structures is too obvious to require description.

In Mammals the end of the large intestine, where it passes into the small intestine, is usually enlarged to form the cæcum. In Man there is at first no cæcum (fig. 143, A-C), then a simple conical projection appears (fig. D); later the cæcum lengthens, but the terminal portion does not keep pace with the growth of the base, and consequently becomes much narrower in calibre. The basal portion eventually grows so large that it is commonly called the cæcum, while the true cæcum is designated as the vermiform appendix. Several of the stages in the development of the human cæcum are permanently retained in the adult stage in certain Mammals. It is not known whether the so-called vermiform appendix of the Wombat is, as in the higher Primates, a remnant of an originally elongated apex of the true cæcum.

In some Armadillos the cæcum is distinctly bilobed, and in *Cyclothurus didactylus* there are two distinct cæca. In addition to a capacious true cæcum, Hyrax possesses a pair of simple conical cæca in the large intestine.

In most Birds there are two cæca of variable length at the commencement of the large intestine.

A cæcum is usually stated to first appear in Reptiles, where it never attains a large size; but Huxley has described and Howes has figured a representative of it in the Frog.

A simple rectal gland is found in Elasmobranchs.

Endodermal Muscles.—Muscular processes arising from the endodermal cells have been demonstrated by Jickeli in *Hydra*; these run transversely round the body, as opposed to the longitudinal direction of the similar fibres of the ectodermal cells. Endodermal muscular fibres have been demonstrated in the *Actiniæ* by the brothers Hertwig.

Respiratory Organs of Invertebrates.—In but few Invertebrates does the alimentary tract function directly in respiration. The endoderm lining the general cavity of the body in Actinozoa is, however, probably largely concerned in respiration, especially in such forms as *Edwardsia*, *Cerianthus*, and *Peachia*, which live imbedded in the sand.

Respiration probably occurs all along the intestine in *Proneomenia*, and along the rectum in *Neomenia*.

The anal respiration of many Crustacea is, as has already been stated (p. 109), really proctodæal.

The respiratory trees of most Holothuroidea are probably of hypoblastic origin. In other Echinoderms the ambulacral system is partially respiratory.

Chordata.—The anterior portion of the chordate mesenteron is mainly devoted to respiration; this may appropriately be termed the branchial region, or, more shortly, the pharynx.

In most Chordata several pairs of wide lateral pouches arise from the sides of the pharynx and come into close contact with the external skin. There is apparently a slight invagination of the latter to meet the former; an absorption of the applied membranes results in the formation of lateral slits (branchial or visceral clefts), by means of which the cavity of the pharynx is put into direct communication with the exterior.

Delicate processes of the hypoblastic epithelium covering the intermediate bars (branchial or visceral arches) constitute the gills or branchiæ. These are richly supplied with blood by the branchial vessels (p. 226). True gills, however, are never developed in the Amniota at any period of life.

Almost invariably the anterior (hyomandibular) visceral cleft is the first to appear, the remainder appearing in order from before backwards.

The worm-like *Balanoglossus* has pharyngeal gill-slits which arise in the same manner as those of Vertebrates; for a long time there is only one pair, but subsequently they are repeated in pairs, increasing in number with the increase in the size of the body [Bateson]. The collar at the base of the proboscis grows backward as an opercular fold to a variable extent in different species of *Balanoglossus*, but it never extends beyond three gill-slits. The enclosed cavity is termed the atrial cavity by Bateson.

Van Beneden and Julin have shown that all Ascidians have but a single pair of visceral clefts, which arise as a pair of pharyngeal pouches met by corresponding epiblastic depressions. This condition is permanently retained by the interesting tailed form *Appendicularia*. In all other Ascidians the gill-clefts fuse together to form a single chamber (peribranchial cavity or atrium), which almost entirely sur-

rounds the pharynx (branchial sac). It is probable that the atrial pore is the persistent opening of the fused gill-slits. The atrium may be formed more especially from the hypoblastic or the epiblastic portion of these clefts. The numerous and usually irregular orifices (stigmata) in the pharynx clearly do not correspond with the gill-slits of higher forms, but are merely secondary perforations. We may say, with these authors, "the Tunicata are Chordata with a single pair of branchial clefts, while the Vertebrata are furnished with several, and the Cephalochorda (*Amphioxus*) with a great number."

In *Amphioxus* also a single pair of gill-slits first makes its appearance. This is subsequently followed by a large number (70-100), which slant obliquely from before backward. In the young form the gill-slits open directly to the exterior, but they are eventually covered by a pair of dorsal folds of skin which grow downwards, leaving a space between themselves and the gill-slits (the branchial chamber or atrium). The two flaps of skin meet below the body and fuse throughout their whole extent except at one spot, the branchial or atrial pore. It will be readily apparent that the branchial chamber of *Amphioxus* is by no means homologous with that of *Ascidians*.

The number of gill-clefts never exceeds eight pairs in the Vertebrata. There are seven in the Cyclostomi and in *Hexanchus*, eight in *Notidanus* (*Heptanchus*), but six in all other Elasmobranchii; amongst the Teleostei a further reduction in the number of clefts occurs, owing to the suppression of the hyoid pair.

The first cleft succeeding the mouth is termed the hyomandibular or hyoid cleft (spiracle), as it lies between the mandibular and hyoid arches. The second is correspondingly the hyobranchial or first branchial, and is bounded by the hyoid and the first branchial arches. The remaining slits are the branchial clefts.

Dohrn finds that the pair of ciliated grooves which lie in front of the gill-pouches in the Lamprey (fig. 142) is developed in the same manner as the branchial pouches, but an external opening is never acquired. This supposed lost pair of visceral clefts is termed by Dohrn spiracular or thyroidean.

Primitively all the visceral clefts were undoubtedly respiratory in function, and in many Elasmobranchs the mandibular border of the spiracle bears a rudimentary gill. In *Chimæra*, some Ganoids, and many Teleosts, the hyoid border of the second cleft possesses only a rudimentary gill (opercular pseudobranch), which undergoes all stages of degeneration amongst the Teleosts, all the anterior gill-filaments having atrophied. The posterior gills have a tendency to disappear in Teleosts, the greatest reduction occurring in

Amphipnous euchia, in which one branchial arch alone bears branchial filaments.

The gill-clefts in the Cyclostomes and Elasmobranchs are left quite exposed on the surface of the neck, but in Chimæra, Ganoids, Teleosts, and Dipnoi they are protected by a fold of skin (operculum), supported by skeletal elements; the branchiostegal membrane and its supporting skeleton are derivatives of the hyoid arch. In some forms the border of the operculum fuses with the skin of the body, merely leaving a small orifice on each side leading from the branchial chamber.

In Amphibia the hyoid pharyngeal pouch never communicates with the exterior, but persists as the Eustachian recess. In larval life four, or rarely three (some Urodela), branchial clefts appear. The first, second, and third branchial arches develop external gills which may be covered by epiblast. These usually atrophy, and internal, probably hypoblastic, gills are developed on each side of the three branchial clefts. The internal gills are always lost, but in some Urodeles the external gills are retained throughout life. Cope has recently stated that the Siren loses and then re-acquires its external gills. Other Urodeles, which normally lose their gills when adult, may, however, become sexually mature while still retaining their gills (Axolotl).

An opercular fold grows back from each hyoid arch in Anura, and fusing above and below with the skin of the body, envelops the gills within a branchial chamber. At first the branchial chambers open widely to the exterior by an orifice on each side; these persist in Dactylethra, according to Huxley. In Bombinator and certain other forms the openings of the branchial chambers unite to form a single ventral orifice. In the majority of Anura (Rana, Bufo), the two branchial chambers communicate by a ventral canal, and the opening of the right chamber is closed up, leaving a single asymmetrical pore on the left side.

External gills are present in some Ichthyopsida, but they have already been alluded to (p. 109).

The external gill filaments of Elasmobranch embryos arise as simple elongations of the posterior lamellæ of each arch, the anterior not elongating at all. Dohrn finds that yolk is present in these filaments and in their veins, and also in the posterior branchial vein and the efferent arteries, but never in the heart or in the branchial artery. It would thus appear that these elongated filaments serve also to absorb the yolk.

In none of the Amniota do the visceral clefts bear gills at any period of life. In all forms there are four pairs of clefts, the last two being very small in Mammals. The visceral arches between the clefts are well marked (fig. 145, k' , k''), each possessing a central artery; but in Mammals the last cleft is not bounded by a posterior arch. In Man, at least, none of the visceral clefts are actually perforated [His], and the fourth and fifth external visceral furrows are withdrawn into a fold or sinus of the neck (sinus præcervicalis), (figs. 146, 147).

The visceral clefts close up and entirely disappear, with the exception of the first (hyoid or hyomandibular), which, as has already been described (151), persists as the Eustachian tube and tympanic cavity.



FIG. 145.—HEAD OF EMBRYO RABBIT OF TEN DAYS. Magnified 12 diameters. [From Kölliker.]

a. eye; at. atrium or primitive auricle of the heart; b. aortic bulb; k' , k' , k'' . first (mandibular), second (hyoid), third (1st branchial) visceral arch; m. mouth; o. superior maxillary process, and u. inferior maxillary (mandibular) process of the right side; s. mid-brain, which forms the anterior extremity of the body; v. anterior portion of head and fore-brain; v. ventricle of the heart.

Intestinal Respiration.—Many Teleosts swallow atmospheric air, which passes along the alimentary canal and is ejected by the anus. There can be no doubt that this is a method of supplementary respiration. In these forms the hypoblast of the intestine is a respiratory tissue. Gage finds that the papillate mucous membrane of the pharynx of the American fresh-water Turtle, *Aspionectes spinifer*, is distinctly respiratory in function, but this does not appear to hold good for other forms [Haswell].

Air-Bladder.—A tubular diverticulum grows out from the dorsal side of the œsophagus or stomach in most Ganoids (fig. 152, A, a, b) and Teleosts. In the Salmon and Carp [Von Baer] it arises just in front of the liver, and slightly to the right side. It grows backwards, and in some cases forwards as well. Excepting in some Teleosts this structure persists as the air-bladder.

It is possible that the primitive diverticulum from the mesenteron, which afterwards developed into the air-bladder, was originally connected with secretion. A

small sac of unknown function occurs on the dorsal wall of the gullet in some Elasmobranchs.

The gases contained in the alimentary canal, and also, perhaps, air swallowed for respiratory purposes, would naturally tend to collect in a dorsal diverticulum. A hydrostatic apparatus would thus be formed, the muscular walls of the sac (air-bladder) enabling the quantity of the contained gases to be regulated.

In some Fish (Physoclysti) the duct (pneumatic duct) by means of which the air-bladder communicates with the alimentary canal becomes closed; and in others, as in the Pleuronectidæ, the air-bladder may entirely disappear.

In the Physoclysti the amount of gas in the air-bladder is regulated by diffusion through a network of blood-vessels. Under some conditions the fish may respire with the air secreted in the air-bladder by its own blood-vessels; but this is a purely accessory and temporary mode of respiration.

The air-bladder in some Ganoids and Teleosts, and notably in the Dipnoids, is cellular and very vascular, and atmospheric air is in some of them known to be sucked in through the mouth, so that the air-bladder functions like a true lung.

In Gurnards and other Teleosts the air-bladder is used in making grunting sounds. In many Teleosts the air-bladder functions as an accessory auditory organ, either by impinging directly on the vestibulum of the internal ear, or by being indirectly connected with it by means of a chain of ossicles. The auditory function is most highly developed in the Siluroids, in which group the air-bladder becomes strangely modified, and may come anteriorly into close contact with the body-wall immediately behind the shoulder-girdle. The body-wall may become extremely thin at this spot, so as to form a regular tympanum. It is interesting to note that this tympanic membrane, like the tympanum of the ear, is lined externally by epiblast and internally by hypoblast.

In no organ of Vertebrates is there so varied a change of function as there is in this enteric diverticulum of Fishes.

Lungs.—The lungs are developed from the ventral wall of the œsophagus immediately behind the pharynx as an elongated groove, which abruptly terminates posteriorly (fig. 143, A, *lg*). This ventral groove becomes constricted off from the œsophagus, except at its anterior end (glottis), where it still retains its connection with the pharynx (fig. 143, *la*). The blind slightly swollen extremity of the newly formed tube is the rudiment of the lung, and the duct is the trachea.

The lung very early exhibits a bilobed character (figs. 141, *c*; 146, *c*, *l*). Some observers state that it is from the first distinctly paired.

In most Amniota the surrounding splanchnic mesoblast becomes greatly thickened, and the hypoblastic sac-like lungs burrow into the stroma, dividing and subdividing as they advance. Eventually an extremely ramified system of tubes is formed in Mammals, each ultimate branch of which being terminally distended into a sacculated ampulla (infundibulum).

The primitive sac-like character of the lungs (fig. 143, B) is retained in the Amphibia and most Reptilia, the walls being merely infolded to give increased respiratory surface.

In the Chameleons variable branched prolongations of the lungs project freely into the body cavity. Analogous diverticula appear in the embryos of Birds, and ultimately form the air-sacs. Prolongations from the latter pass into many of the bones in most Birds, the penetration of these delicate sacs into the bones being due to bone-absorption consequent on pressure.

The cartilaginous rings of the bronchi and trachea and the cartilages of the larynx are of mesoblastic origin.

The air-bladder of the Dipnoids is clearly homologous with the same organ of other Fishes, but in this remarkable group of animals the air-bladder is distinctly double; its walls are greatly infolded ("spongy" or "cellular") and very vascular; the blood supply is taken directly from the last aortic arch, and not from the celiac artery, the blood being returned directly to the heart, and not to the liver, as in other Fishes; lastly, the wide pneumatic duct opens on the ventral wall of the throat (the same also occurs in the Ganoid Polypterus). In all these points the air-bladder of the Dipnoi resembles the lungs of Amphibia. From these facts it is usually concluded that lungs are directly derived from the air-bladder of Fishes.

Minot, however, has suggested that the lungs have been evolved by the modification of a pair of gill-pouches, which do not break through in the neck, but grow down into the thorax (figs. 141, c, 146, c, l).

Albrecht considers it erroneous to homologise dorsal with ventral organs, and points out the difficulty of the migration of the dorsal air-bladder to a sub-oesophageal position. In the Gymnodont Teleosts, in addition to the dorsal air-bladder, there are ventral air-sacs proceeding from the oesophagus, by means of which these fishes can inflate themselves. These sacs are considered by him as homologous with lungs, and heterologous to the dorsal air-bladder. The air-bladder of Polypterus would therefore be the homologue of the lungs. Dorsal diverticula from the oesophagus opposite the larynx may normally (Pig) or abnormally (Man) be present.

Tongue.—Born finds that in the Pig the tongue is developed from the anterior portion of the ventral floor of the pharynx. The space between the ventral ends of the first and second visceral arches is at first depressed; but later a longitudinal ridge grows up, separated from the arches on each side by a groove. The anterior portion of this ridge grows forward and becomes the free part of the tongue. The tongue does not extend back beyond the second arch, but the posterior portion of the ridge projects between the third and fourth arches and develops the epiglottis. As Minot points out, the epithelium covering of the tongue is thus hypoblastic in origin.

If the above statement is correct, the taste-buds on the papillae are hypoblastic sense organs. The gustatory goblet-cells on the tongue of Amphibia possibly have a similar origin. The goblet-shaped organs in the mouth and pharynx of Fishes may have a similar function, but those of the mouth appear to be homologous with similar organs situated in the skin. Macallum has very recently recorded the occurrence of taste-buds in the oesophagus of the Sturgeon; he also states that he has found them in *Amphioxus* as far back as the opening of the hepatic caecum.

According to His, the tongue in Man has a double origin. From the anterior region of the ventral space (mesobranchial area), between the visceral arches of an early embryo, a small round projection (tuberculum impar) is formed; behind this are a pair of folds (furcula), which eventually will form the epiglottis. The ventral portions of the second and third arches grow towards their fellows of the opposite side between the tuberculum and the furcula. The basal growths of the arches form the roots of the future tongue, and unite together behind the tuberculum impar;

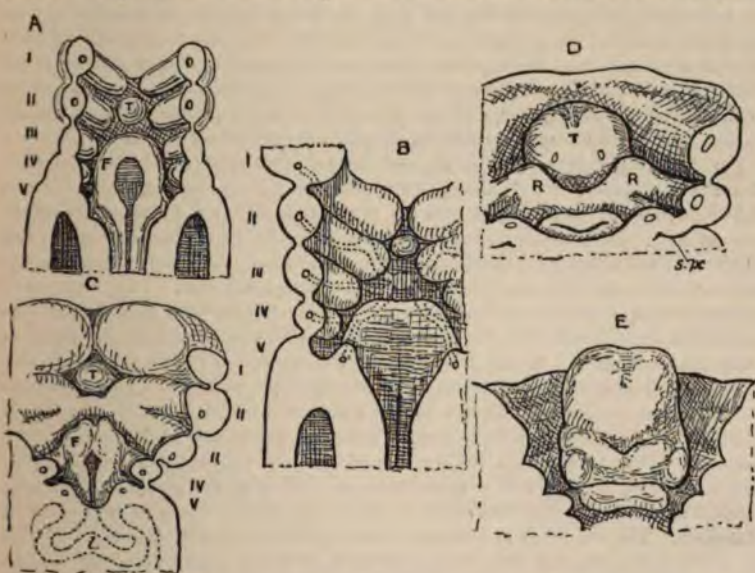


FIG. 145.—DIAGRAMS ILLUSTRATING THE VISCERAL ARCHES AND DEVELOPMENT OF THE TONGUE IN THE HUMAN EMBRYO. [After His.]

Seen from above, the dorsal (posterior) wall of the pharynx being supposed to be cut away. In B, the branchial blood-vessels are indicated.

F, furcula; I, lungs; R, roots of the tongue; s.pc, sinus præcervicalis; T, tuberculum impar, body of the tongue in D; 1-5, visceral arches.

the median pit between these structures is the rudiment of the median lobe of the thyroid body. The tongue is formed by the fusion of the two roots with the tuberculum.

Thyroid Body.—The generally received view of the significance of the thyroid body has already been mentioned (p. 172).

In the Lamprey (fig. 142) the thyroid body arises as a wide diverticulum from the floor of the anterior portion of the pharynx. The orifice becomes restricted to a pore and eventually disappears. During larval life it consists of a median ciliated portion communicating with a pair of complicated lateral glandular sacs.

In some higher forms the thyroid is stated to develop as a tubular diverticulum or solid down-growth from the anterior region of the pharynx, which later becomes bilobed. Subsequently it is quite detached from the pharynx, and is produced into

a number of hollow or solid processes, between which connective tissue septa and blood-vessels enter.

Born reconciles various conflicting observations regarding the origin of the thyroid body in Mammals by finding that, according to his investigations, the organ has a double origin. An unpaired portion arises as an invagination from the floor of the pharynx opposite the front edge of the second visceral cleft. It separates from the pharyngeal epithelium, expands laterally, and migrates backwards. The other portion of the thyroid is derived from the paired remnants of the fourth visceral clefts. These are at first somewhat pear-shaped hollow sacs, but on becoming connected with the central portion they acquire a spongy interior. Pischelis confirms Born's statements from his researches on the Pig, Rabbit, and Birds. His finds, in the human embryos, that the median thyroid rudiment arises as a hollow diverticulum between the third visceral arches, and that the lateral portions are evaginated from the posterior end of the pharynx near the glottis (fig. 147, *l.thyr*). The several parts become separated from their parent tissues and sink into the deeper portion of the neck. The duct of invagination of the median portion persists for some time as the ductus thyreoglossus (fig. 147, *d.thyr*). The foramen cæcum, cornu medium, and the various bursæ which may be present in the adult are rudiments of this duct.

The last investigation on the thyroid body is that of De Meuron, who finds that the median element is always (Elasmobranch, Frog, Lizard, Fowl, Sheep, and Man) developed from a median pit in the pharynx at the level of the second visceral arch. He homologises the supra-pericardial bodies of Elasmobranchs [Van Bemmelen] and Amphibia [De Meuron] with the accessory or lateral thyroid bodies of the Amniota (the left alone occurs in *Acanthias* and *Lacerta*). The structure of both resembles that of the median element. These bodies arise as a pair of diverticula behind the sixth branchial cleft (seventh visceral), which is imperfectly developed in many Elasmobranchs. It may be concluded that these represent a degenerate pair of gills as in *Heptanchus*, in which there are seven branchial clefts, the supra-pericardial bodies are absent. In the higher Fishes and larval Amphibia the lateral rudiments of the thyroid develop directly from the pharynx behind the last (fifth) branchial cleft. Owing to a further reduction of the clefts, which also disappear without leaving a trace and a consequent shortening of the pharynx, the lateral thyroids appear to develop from the fourth branchial cleft; this is most marked in Mammals. The similarity in structure of the fully-developed lateral thyroids with the median element and their close connection in adult Mammals rather tend to support Dohrn's hypothesis concerning the primitive condition of the median thyroid, i.e., that it represents a pair of degraded hyoid clefts.

Thymus Gland.—Maurer finds that in the embryo Trout the thymus takes its origin from four thickenings of the epithelium of the visceral clefts on each side of the body, a rudiment being situated in the dorsal angle of each of the four clefts. A proliferation of the epithelium takes place, and the four rudiments on each side become fused together. Each lateral thymus gland sinks into the underlying meso-blast and takes on the character of a lymphatic gland.

Dohrn states that there is primitively one thymus rudiment for each branchial cleft in Elasmobranchs, but the fifth disappears in the Sharks. The separation of these rudiments from the epithelium is due to the shortening of the clefts and the bending of the visceral arches. The parts thus isolated gave rise to a new organ, the thymus, which was afterwards transmitted by heredity to higher Vertebrates.

In the Pig, according to Born, the thymus arises as a pair of ventral evaginations from near the inner openings of the third pair of visceral clefts, the outer portions of which atrophy. The end of the thyroid rests against the pericardium at the spot where the aorta leaves it. The central cavity disappears, and many branches grow out from the solid cord, mainly in the direction of the heart.

His finds in the human embryo that the primary (epithelial) rudiment of the

thymus arises from the epithelium of the inner portion of the fourth, third, and partly also of the second visceral clefts. These parts become massed together and separated from the outer skin (fig. 147, *thm*). He asserts that it is developed from the epidermis and cannot be regarded as a hypoblastic structure, since in Man none of the visceral clefts become perforated.

It is evident that the function of the gland in the Amniota is secondarily acquired, and that it is a degraded epithelial organ, which, from its relation to the gill-clefts in Fishes, may possibly have been some form of sense organ.

De Meuron has also studied the development of the thymus. In Ichthyopsida and Sauropsida it arises as solid thickenings of the epithelium of the dorsal side of the branchial clefts. In Fishes it arises from the first four branchial clefts, in the Lizard from the second, third, and fourth, and in Birds from the third and fourth visceral

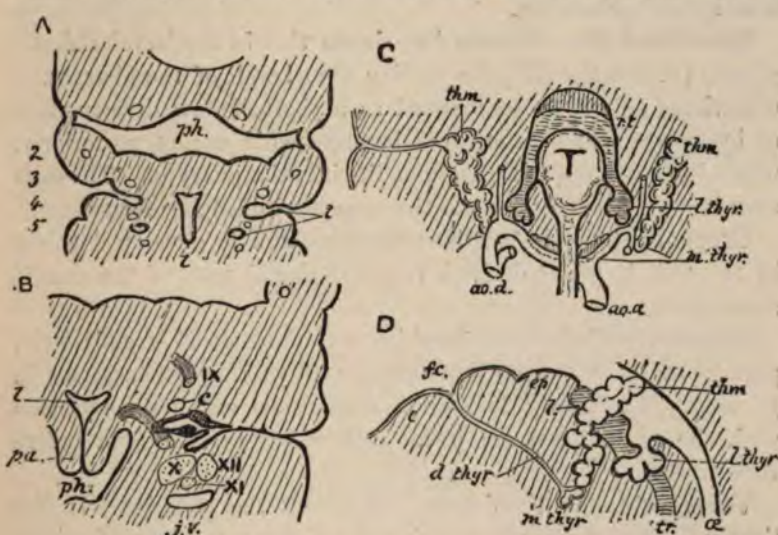


FIG. 147.—DEVELOPMENT OF THE THYMUS GLAND AND THYROID BODY IN THE HUMAN EMBRYO. [After His.]

A. Transverse section through the hinder portion of the head. B. Transverse section through the larynx of an older embryo. C. Profile reconstruction of the thyroid and thymus glands, seen from below. D. The same seen from the side. *ao.a.*, *a.o.d.*, ascending and descending aorta; *c.*, carotid artery; *d.thyr.*, ductus thyroglossus; *ep.*, epiglottis; *f.c.*, foramen cecum; *j.v.*, jugular vein; *l.*, larynx; *l.thyr.*, lateral thyroid rudiment; *m.thyr.*, median thyroid rudiment; *o.*, oesophagus; *p.a.*, plicae aryepiglotticæ; *ph.*, pharynx; *r.t.*, roots of the tongue; *t.*, tongue; *thm.*, rudiment of the thymus gland; *tr.*, trachea; *IX.*, glossopharyngeal; *X.*, vagus; *XI.*, hypoglossal; *XII.*, spinal accessory nerves; 1-5, visceral arches.

clefts. In the last three groups the thickening of the third cleft is the largest. In Anura the second visceral cleft alone develops a thymus. The history of the thymus is very different in Mammals; dorsal rudiments are developed, as in Birds, from the third and fourth visceral clefts, but nearly the whole of the adult organ is derived from a ventral caecum from the third branchial cleft.

Gustatory Organ of Amphioxus.—The organ usually known as the olfactory organ of *Amphioxus* consists of an outer ciliated sac opening to the exterior and also into an inner sense-organ, which again communicates with the mouth. Hatschek finds that the whole organ is developed from the left of a pair of archenteric diverticula in front of the mouth, and that it is therefore of purely hypoblastic origin. It probably is an organ of taste. Hatschek and Dohrn are inclined to homologise it with the hypophysis.

Excretory Organs.—The only excretory organs which appear to be of hypoblastic origin are the paired urinary tubes which occur in Amphipods. They arise from the extreme hind-end of the mesenteron, there being a distinct break of continuity when the latter ceases and the hind-gut (rectum) begins [Spencer]. Their development is unknown.

Skeletal Structures.—Notochord.—The primitive axial supporting rod or skeleton (notochord), or chorda dorsalis, which is peculiar to the Chordata, and from which they derive their name, is of hypoblastic origin.

Hemichordata.—Bateson has shown that in the larval *Balanoglossus* (*B. kowalevskii*) the median dorsal wall of the pharynx is constricted off and grows forward as a short hollow diverticulum of hypoblast, which afterwards becomes solid except posteriorly, where its lumen opens throughout life into the pharynx. The cells soon become vacuolated as in the notochord of higher forms.

Urochordata.—In Ascidians the notochord is developed solely in the tail, it being derived from the dorsal wall of the caudal archenteron.

Cephalochordata.—In *Amphioxus* the notochord is, as it were, pinched off from the median dorsal wall of the archenteron (fig. 56 *neh*). Ultimately its folded appearance and its connection with the archenteron are lost. It is constricted off from before backwards.

Vertebrata.—In the lower Vertebrates the notochord is distinctly derived from the dorsal wall of the mesenteron (archenteron). Hertwig's researches on the development of the Newt (*Triton*) show that the dorsal hypoblast (usually referred to in this book as invaginated hypoblast and the chorda entoblast of Hertwig and others) not only is distinctly columnar, as opposed to the rounded ordinary hypoblast cells, but it also lines a distinct groove (fig. 148). The two sides of the notochordal groove, as it may be termed, come together and form a solid rod of cells, the arrangement of which gives no indication of their origin. The notochordal groove is scarcely apparent in the Frog.

Mitsukuri and Ishikawa have demonstrated that the notochord in the Snapping Turtle (*Trionyx japonicus*) (fig. 149) is developed in a manner perfectly comparable with that of the Newt. Indications of a similar origin of the notochord are found in Lizards, and notably in Mammals.

In Birds the axial hypoblast very early becomes converted into

the rudiment of the notochord, and this may occur almost before the permanent hypoblast can be recognised as such; hence the supposition of some authors that the notochord was derived from the mesoblast.

FIG. 148.—TRANSVERSE SECTION OF THE DORSAL PORTION OF AN EMBRYO NEWT (TRITON). [After O. Hertwig.]

a. mesenteron; ax.hy. axial hypoblast in process of forming the notochord; b.c. coelom (body-cavity); ep. epiblast; hy. digestive hypoblast; n.p. neural plate; so.m. somatic mesoblast; sp.m. splanchnic mesoblast.



The rudiment of the notochord consists of a solid rod of cells lying between the neural tube and the mesenteron. Posteriorly it is connected with the fusion of the layers which occurs at the

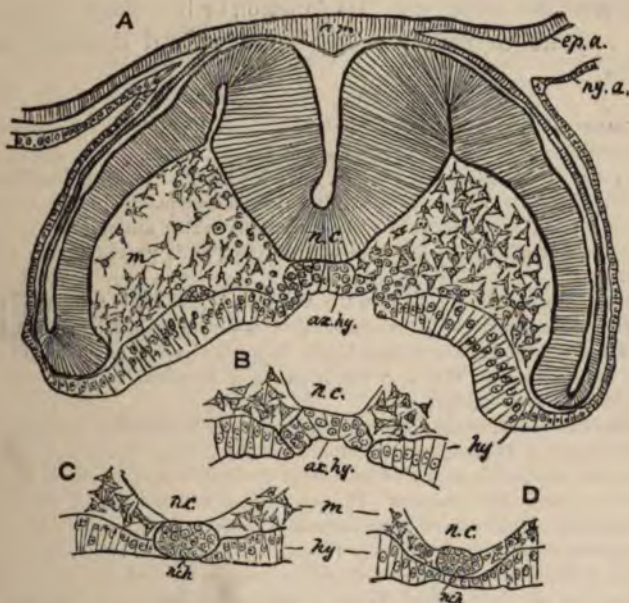


FIG. 149.—FORMATION OF NOTOCHORD IN TRITON. [After Mitsukuri and Ishikawa.]

A. Transverse section through the head region before the closure of the neural groove. B. D. Portions of successive sections of the same embryo. The shading of the epiblast is purely diagrammatic.

am. amnion; ax.hy. axial hypoblast; ep.a. epiblastic, and hy.a. hypoblastic layer of amnion; hy. hypoblast; m. mesoblast; n.c. neural canal; nch. notochord.

dorsal lip of the blastopore (fig. 62), or, when there is no distinct blastoporic passage, as in the Fowl, it passes into the primitive streak. At a later stage the notochord terminates anteriorly

behind the infundibulum, its extremity being often recurved. Posteriorly the notochord terminates at the end of the tail.

A definite sheath (*elastica limitans interna*) is soon formed as a secretion from the peripheral cells of the notochord. The cells of the notochord become vacuolated, so that the notochord has a spongy appearance; a few nuclei surrounded by a little protoplasm remain attached to some of the meshes of the network (figs. 150, 152, 173, 175, *ch*).

The notochord and its sheath are replaced in most Vertebrates, leaving only a small rudiment, as will be mentioned in the description of the development of the vertebral column (pp. 196-199).

Sub-Notochordal Rod.—A solid rod of cells is developed from the dorsal wall of the alimentary canal in Ichthyopsida after the formation of the notochord (figs. 150, 173, 175, *x*).

This sub-notochordal rod, as it is termed, has about the same extension as the notochord. Its function or homology is unknown, but it appears to persist as the sub-vertebral ligament in the Sturgeon.

Significance of the Notochord.—Few embryological problems are more obscure than the probable phylogenetic significance of the notochord. The embryological evidence points to its hypoblastic origin. We are justified in assuming the primitive, or at all events the archaic, nature of its development in the *Amphioxus* (fig. 56) and the Newt (fig. 148). The variations which are met with in other Vertebrates can be reduced to the type of the Newt, as is proved by the *Chelonia* (fig. 149).

The development of the urochord in the Ascidians is manifestly a degraded process.

The restricted notochord of *Balanoglossus* develops in an essentially similar manner to that of *Amphioxus*, but the central lumen is retained for a much longer period. It is interesting to note that in some Amniota a transient canal occurs at the posterior end of the notochord.

Upon an examination of the figures given by authors illustrating the development of the notochord in *Balanoglossus*, *Amphioxus*, the Newt, *Chelonia*, Lizards, and Mammals, the conclusion seems to be almost inevitable that we must regard the notochord as a secondary structure. It may be that the ancestor of the Chordata possessed a longitudinal groove along the neural aspect of its alimentary tract, which may have had some special secretory (? mucous) function. The extremely early acquisition of distinctive histological characters may be recalled in this connection.

The closure of the notochordal groove in ontogeny at the time of the constriction off of the archenteric diverticula from the mesenteron is suggestive of phylogenetic synchrony.

It is not difficult to imagine that a rod of cells, even though containing at first a small lumen, might form a mechanical support to the body which would prove of considerable value, and, being internal, it would grow with the growth and requirements of the animal.

Urinary Bladder.—The urinary bladder is properly speaking a hypoblastic organ, but it is more convenient to deal with it at the same time as the uro-genital ducts (p. 259).

CHAPTER VII.

ORGANS DERIVED FROM THE MESOBLAST.

HOWEVER it arises, the mesoblast gives rise to the deeper layer of the skin, *i.e.*, the derma or cutis; to the whole of the muscular system in animals higher than the Cœlenterata; to nearly all the internal supporting structures of the body; to the lining membrane of the body-cavity, peritoneum, in the broadest sense of the term: to the whole of the vascular system; to the excretory organs; and to the generative glands.

Indifferent Mesoblast.—Under the term indifferent mesoblast may be classed the general parenchyma of the body of the lowest Metazoa.

In the Porifera, between the two primitive epithelia of the body irregular amœboid cells occur in greater or less abundance, imbedded in a jelly-like matrix. Sollas suggests the appropriate term of archæocytes for such cells. The origin of these mesamœboids has been described; they function in various ways, probably mainly in nutrition, by carrying food-products to various parts of the organism, and in the transportation of waste matter, in this respect resembling the leucocytes of higher animals. Many of the mesamœboids secrete spicules; some develop into muscle-cells; others constitute germ-cells, and some are stated to act as nerve-cells.

The oval or anastomosing stellate cells in the gelatinous tissue of Scyphomedusæ arise mostly from the hypoblast, and the muscular stellate cells of Ctenophora from the epiblast, though some are stated by Chun to be of hypoblastic origin. There may be connective-tissue cells in the fibrillar lamina of Actinozoa.

The mesamœboids enclosed within the spacious segmentation-cavity of larval Echinoderms have many functions to perform; as Metschnikoff has shown, they devour degenerate tissues (see p. 274), and they also secrete the larval skeleton (fig. 16, *m.s.*).

The spongy parenchyma which fills up the space between the

epiblast of the skin and the hypoblast of the mesenteron in Platyhelminths appears to be of mesenchymatous origin. These cells are essentially "indifferent" in character, and Lankester has shown how that in the Leech this tissue, which he terms skeletotrophic, may insensibly pass into blood-vessels and blood-cells on the one hand, or into connective tissues generally on the other. A good deal of the intermediate parenchymatous tissue of Molluscs might be placed in this category.

In higher forms the wandering cells of the body (colourless blood corpuscles, leucocytes), retain their amœboid nature, and probably have diverse functions. The generative or germ-cells may be considered as the least specialised cells in the body.

Dermal Mesoblast.—That mesoblastic tissue which immediately underlies the embryonic epiblast, and which constitutes the derma or cutis of the adult, may be termed dermal or peripheral mesoblast.

Such, for instance, are those mesamœboids which in Echinoderms are enclosed between the lining membrane of the body-cavity and the epiblast. They constitute the main thickness of the body-wall, and are productive of muscles, ligaments, and the calcareous spicules, plates, and spines.

It would be superfluous to enumerate the various aspects which the dermal mesoblast assumes.

The derma of Vertebrates typically consists of—(1.) Connective tissue fibres and elastic fibres. The fibres of the derma in Ichthyopsida are usually arranged in more or less regular vertical and horizontal bundles, whereas those of the Amniota are irregularly felted together. (2.) Pigment cells and wandering leucocytes. (3.) Often a deeper layer of fat cells. (4.) Non-striated muscular fibres; and, lastly, it is penetrated by blood-vessels and nerves from the one side, and by glands and hair-bulbs on the other.

Muscular System.—There is considerable uncertainty with regard to the exact origin of the muscular system of many Invertebrates. In some cases it is wholly or partially mesenchymatous (Echinodermata, Platyhelminths). In the Echinoderms the epithelial cells of the archenteric diverticula are stated by Metschnikoff to possess muscular processes, but it is not known whether these furnish all the muscular elements of the body-wall. The external muscle fibres, which cause the movements of the spines of the Echinoids, are almost certainly not so derived. The muscles are known to be mesothelial in origin in the Earthworm; but even

in the Chætopoda and Arthropoda (?) mesenchymatous elements are stated by some observers to be present, and these may possibly form muscle-cells.

In the Chordata the muscular system is entirely of mesothelial origin, being derived from the somatic and splanchnic layers.

The first muscles to make their appearance in *Amphioxus*

FIG. 150.—TRANSVERSE SECTION THROUGH THE TRUNK OF AN ELASMOBRANCH EMBRYO (*Pristiurus*). [From Balfour.]

al. mesenteron; *ao.* aorta; *mp.* muscle-plate; *mp'.* portion of muscle-plate converted into muscle; *nc.* neural canal; *pr.* dorsal root of spinal nerve arising from the neural crest; *sc.* somatic mesoblast; *sp.* splanchnic mesoblast; *V.v.* portion of the vertebral plate which will give rise to the vertebral bodies; *x.* subnotochordal rod.

The intermediate cell mass connects the dorsal and ventral mesoblast; it is seen on the left-hand side of the figure, between the lines pointing to *x* and *ao.*



(fig. 56, *c*, *m*) are the longitudinal muscles which lie on each side of the notochord; they arise as differentiations of the basal portion of the splanchnic cells of that region.

If fig. 56 is compared with figs. 150 and 175, it will be seen that the great lateral muscles of Elasmobranchs are developed from similar splanchnic cells, and the same may be traced in an early stage in the muscle-plates of the Amniota. In the embryo Bird

FIG. 151.—HORIZONTAL SECTION THROUGH THE TRUNK OF AN EMBRYO FOWL.

The section passes through the notochord and shows the separation of the cells to form the vertebral bodies from the muscle-plates.

ep. epiblast; *l.m.* longitudinal muscles differentiated from the splanchnic portion of the muscle-plate, *m.p.*; *nc.* notochord; *v.r.* vertebral rudiment.



the first-formed muscles have a longitudinal direction, and are divided into segments.

A horizontal section through a portion of the body of an embryo Fowl (fig. 151) on the level of the notochord clearly exhibits the segmented character of the dorsal mesoblast. The section is taken at a stage when the splanchnopleur has differentiated into an inner vertebral rudiment (p. 199) and an outer layer of longitudinal muscles, while the somatopleur is unmodified. A comparison of

this figure with that of *Amphioxus* brings out the fact that the dorsal portion of the body is characterised by a series of mesoblastic pouches, each of which contains an isolated portion of the body-cavity. This primitive character is masked in most other forms, but in all the Chordata the great lateral muscles are developed therefrom.

Balfour terms each mesoblastic pouch a somite, which is the equivalent of a protovertebra of many authors, reserving the name of muscle-plate to the somite after it has given rise to the vertebral rudiment, as it is then entirely metamorphosed into the voluntary muscular system.

The muscle-plates increase in size and extend into the ventrolateral wall of the embryo. The splanchnopleur is first converted into muscle-cells, the somatopleur becomes implicated later.

The musculature of the limbs early appears as dorsal and ventral bands, which originate from processes from the muscle-plates (fig. 103, *mp.l*). These become segmented off from the muscle-plates, which then pass into the ventral wall of the body.

We may conclude that the primitive continuous lateral fin was put in motion by muscular processes from each muscle-plate; and that when the limbs were differentiated from the fin, some, at least, of the segmental muscles were so grouped as to form the muscles of the limbs.

The muscles of the head, including the eye-muscles, arise from the walls of the cephalic somites (p. 140), in the same manner as those of the body.

The transformation of an epithelial-cell into a muscle-cell occurs by the differentiation of the protoplasm into the contractile fibrils either at one side or peripherally; in the former case the original nucleus is lateral, in the latter it is situated in the centre of each cell.

Dermal Skeletal Structures.—Invertebrates.—Mesodermal exo-skeletal structures scarcely occur amongst the Invertebrates. The Holothuroidea have thin perforated calcareous plates or spicules imbedded in their skin; all the other Echinoderms are characterised by an extensive development of solid calcareous plates and spines.

Chordata.—The dermal skeletal elements of the Chordata may be conveniently reduced to one type, namely, to a placoid scale, the development of which has already been noticed (p. 103). Minute placoid scales or denticles scattered over the skin constitute the shagreen of Elasmobranchs. Each denticle has a basal plate formed of bone.

The large dermal plates of Ganoids and some Teleosts are by some regarded as formed by the fusion of the basal plates of numerous denticles, the polished surface of the plate being due to a deposit of enamel.

The thin scales of *Amia*, most Teleosts, (and Dipnoi) are undoubtedly the somewhat degraded representatives of the bony plates of their Ganoid ancestors. In many cases the supposed epiblastic portion (enamel) of the scales and dermal plates atrophies or is undeveloped.

The dermal plates, which have a purely mesoblastic origin, form the group of bones known as membrane bones (see also p. 210). To this category belong the parosteal elements of the skull, and the "clavicles" of Teleosts.

Recent Amphibia are peculiarly deficient in a dermal exo-skeleton. Bony plates occur in skin of the back in *Ceratophrys dorsata* and *Ephippifer aurantiacus*, and scutes in the *Cæcilians*.

The scutes (often called scales) of *Lacertilia* and *Crocodilia* are formed as ossifications in the derma. The scale-papilla may be best compared to an extremely flattened feather-papilla, which, like the latter, is set at an angle within a follicle. The mesoblastic core ossifies, and the overlying Malpighian layer of the epiblast possibly in some cases deposits a layer of enamel.

Among recent *Reptilia* the *Chelonia* have by far the most developed dermal exo-skeleton, which forms a dorsal carapace and a ventral plastron. Parosteal riblike bones (splints) occur in the ventral wall of the abdomen of *Hatteria* and *Crocodilia*. Similar ossifications are occasionally present in the intermuscular septa of Teleosts.

The bony plates which occur in the sclerotic in Birds, Reptiles, and many Fishes belong to this category.

No dermal skeletal structures occur in the trunk of Birds, and but few in Mammals, the most noticeable being the extensive scutes of the *Armadillos*.

Mesoblastic Endo-Skeletal Structures. — Invertebrates. —

The supporting or endo-skeletal structures of the Invertebrates are almost universally of epiblastic origin. The following are the chief mesoblastic formations.

The spicules of Sponges arise from a single mesamœboid; when bundles of delicate spicules (trichites) occur, the whole mass is developed from a single cell.

The exact origin of the gelatinous supporting tissue of *Cœlenterates* (mesogloea) has not been fully made out. The calcareous skeleton of the *Hexacoralla* and the calcareous spicules of the *Octocoralla* are secreted by cells derived from the ectoderm.

The horny axial skeleton of the Gorgoniidae, the alternate horny and calcareous axis of the Isidinae, and the calcareous stem of *Corallium*, may prove to be epiblastic, like the horny axis of the Antipathidae.

In the free-swimming larvæ (Plutei, &c.) of the Echinoidea, Ophiuroidea, and Crinoidea, a calcareous spicular skeleton is secreted by the mesamœboids (fig. 16, m.s.).

A cartilaginous axis supports the branchial plume of the Serpulæ.

True cartilage occurs in the Cephalopods and in connection with the odontophore in Gasteropods; the former are the only Invertebrates in which the brain is protected by a cartilaginous brain-case.

Chordata.—An endo-skeleton which supports the body and grows with its growth is one of the principal characteristics of the Chordata as a whole. It would perhaps be hardly too much to say that the possession of this and the adaptive axial skeleton was probably the main factor in the evolution of the group. The endo-skeleton of the Chordata includes an axial and appendicular elements. The former consists primitively of the notochord with its skeletogenous sheath, and secondarily of the vertebral column and the cranium.

The appendicular skeleton is derived from the primitive supports of the locomotory organs (fins). These at first were entirely independent of the axial skeleton, but a more or less intimate connection has subsequently been acquired with the latter.

Other structures have appeared in the walls of the body which have all come to be connected with the axial skeleton; for example, the ribs in the somatopleur of the trunk, the internal branchial visceral bars in the splanchnopleur of the pharynx, and the labial cartilages of the face.

Vertebral Column.—The notochord with its sheath persists as the axial skeleton in Amphioxus, the Cyclostomes, Dipnoi, and Selachian Ganoids. In all the higher Vertebrates a skeletogenous sheath is developed round the notochord.

Skeletogenous Sheath of Notochord.—The skeletogenous or cartilaginous sheath of the notochord is developed from a layer of mesoblast cells which range themselves round the *elastica limitans interna* (fig. 152, B). The layer increases in thickness, and forms a continuous unsegmented tube of fibrous tissue with flattened concentrically arranged nuclei. Outside this layer another sheath is developed, variously known as the *elastica limitans externa* or outer sheath of the notochord.

This unconstricted condition of the notochord is retained by the adult Cartilaginous Ganoids and Dipnoi (fig. 153, A). In *Chimæra* there are added thin calcareous rings, which bear no relation to

the neural arches, and are more numerous. In some Elasmobranchs true vertebræ are imperfectly developed.

In all other forms the notochord is serially constricted by the development of true vertebral centra, and is eventually partially or entirely replaced by the mesoblastic vertebral column.

Vertebral Arches and Vertebral Bodies.—In *Amphioxus* the neural canal is merely protected by a sheath of connective tissue; but in the true Vertebrates a series of cartilaginous bars, neural

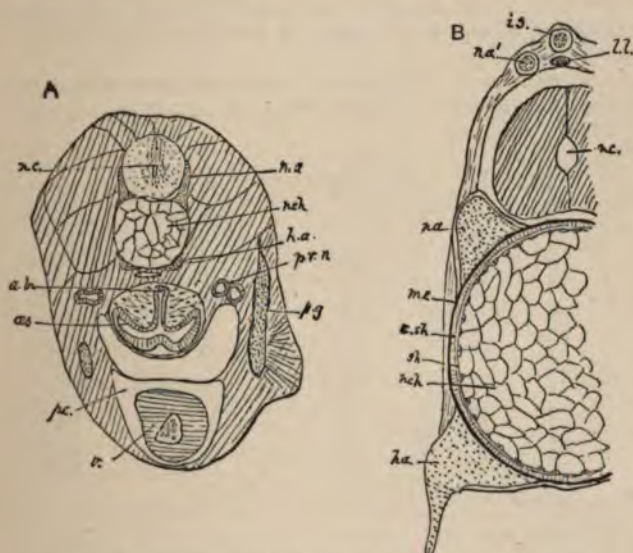


FIG. 152.—NOTOCHORD OF LEPIDOSTEUS. [After Balfour and Parker.]

A. Transverse section through the anterior part of the trunk of an embryo about a month after hatching, showing the connection of the air-bladder with the throat. B. Portion of transverse section through the vertebral column of a larva of 5.5 cm. (through the vertebral region).

a.b. air-bladder; a.c. oesophagus; a.h. pericardium; h.a. haemal arch; h.s. inter-spinous bone; l.l. ligamentum longitudinale superius; m.e. membrana elastica externa; n.a. neural arch; n.a'. dorsal element of same; n.c. neural canal; n.e. neural arch; n.e.s.h. cuticular sheath of notochord; o.s. oesophagus; p.c. pericardium; p.g. pectoral girdle; p.r.n. pronephros; s.h. sheath of notochord (elastica limitans interna); v. ventricle.

The cartilage is dotted; its bony sheath is left blank in B.

arches, are developed, which at first laterally, and then dorsally as well, protect the neural canal.

In the lowest true Vertebrates, the Cyclostomi, the neural arches are irregularly arranged bars of cartilage which do not meet over the neural canal.

Fishes.—In other forms the neural arches first appear as a pair of continuous cellular ridges resting on the skeletogenous sheath of the notochord. A similar ventral ridge, which is better developed in the caudal region, is known as the hæmal ridge (fig. 152).

The neural ridges become enlarged at each intermuscular septum in Fishes. These enlargements are converted into cartilage and form the neural arches. The hæmal arches develop in a similar manner; but it is only in the region of the tail that the hæmal bars unite in the median ventral line to form a true hæmal arch.

In developing and young, and a few adult Elasmobranchs, in certain young and adult Ganoids (Sturgeon, Polyodon, Amia), and in Chimæra, intervertebral or intercalary neural arches are developed. Interhæmal arches are developed in some cases.

The neural arches always make their appearance between the spinal nerves. The interneural arches, when present, usually arise between the dorsal and ventral roots of the nerves.

In the adult Scyllium the dorsal root of a spinal nerve passes through the intercalated cartilage, and the ventral root traverses the neural arch immediately in front.

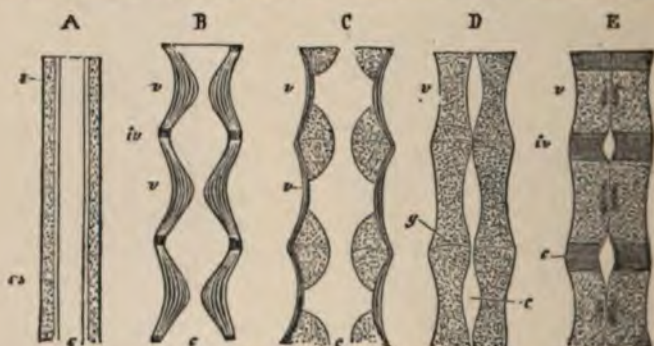


FIG. 153.—DIAGRAM REPRESENTING THE VARIOUS TYPES OF VERTEBRAL COLUMNS IN LONGITUDINAL SECTION. [From Gegenbaur.]

A. Primitive type, with no vertebral segmentation. B. Type of Fishes, with vertebral constrictions of the notochord. C. Amphibian type, intervertebral constrictions of the notochord by intervertebral rings of the cellular sheath. D. Intervertebral constriction of the notochord as in Sauropsida. E. Vertebral constriction of the notochord of Mammals, the intervertebral regions of the cartilaginous sheath being converted into intervertebral ligaments.

n, notochord; cs, cuticular sheath of notochord; iv, intervertebral articulations; iv, intervertebral rings; s, cellular or cartilaginous sheath; v, vertebral regions or bodies of the vertebrae.

The skeletogenous sheath of the notochord also undergoes segmentation, and an annular thickening occurs in the vertebral region (fig. 153, B). This ring becomes converted into hyaline cartilage and encroaches on the notochord, which becomes considerably constricted at these points, but not in the intervals. In the intervertebral regions the sheath of the notochord assumes a fibrous character.

From their mode of formation the vertebrae of Fishes are biconcave (amphicœlous). The gelatinous intervertebral spheres are the degraded remnants of the unconstricted portions of the notochord. Lepidosteus is the only Fish in which the centra of the vertebrae directly articulate with one another, the faces of the bodies or centra of the vertebrae being convex in front and concave behind (opisthocœlous). In this form the bases of the neural and hæmal arches extend into the intervertebral regions,

forming cartilaginous rings. Each intervertebral ring becomes divided into two parts, which will respectively form the anterior face of a given vertebral centrum and the posterior face of that in front of it. There is thus in this Ganoid a secondary intervertebral constriction of the notochord; the latter entirely disappears, except in the tail.

The greater part of the bodies of the vertebræ and of the arches are ossified in Lepidosteus and Teleosts from the membranous perichondrium.

The neural arches rarely unite with their fellows in Fishes, the neural arch being completed above by accessory cartilages and a longitudinal elastic band.

The various forms of Fishes' tails are described later (p. 203).

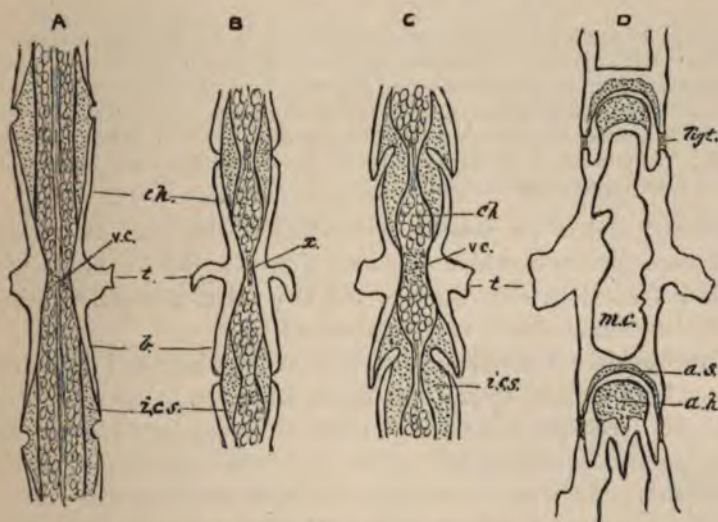


FIG. 154.—LONGITUDINAL SECTION THROUGH THE VERTEBRAL COLUMN OF VARIOUS URODELES. [After Wiedersheim.]

A. *Ranodon sibericus*; B. *Amblystoma tigrinum*; C. *Gyrinophilus porphyriticus* (Vertebrae, 1, 2, 3). D. *Salamandrina perspicillata*.

a.h. articular head, and a.s. articular socket of vertebral body; b. peripheral bony covering of centrum; ch. notochord; i.c.s. intervertebral thickening of cartilaginous sheath; ligt. intervertebral ligament; m.c. marrow cavity; t. transverse processes and ribs; v.c. vertebral cartilage and fat cells; x. vertebral constriction of notochord in *Amblystoma tigrinum* without cartilage and fat cells.

The cartilage is dotted and the bone is left white.

Amphibia.—The Amphibia present us with an interesting series of phases in the development of the vertebral column.

At first, in Urodele larvæ, as in most Fishes, the notochord is vertebally constricted, and the cellular sheath, which is the equivalent of the skeletogenous sheath of Fishes, is early surrounded by a delicate layer of bone which is formed in the investing connective tissue. This biconcave character of the vertebræ is retained by the Cæcilians and the gilled Urodeles.

Later, in the intervertebral regions the sheath becomes greatly thickened, forming deep cartilaginous rings, which constrict and ultimately obliterate the notochord (fig. 154, c).

Finally, an articular cavity is produced by absorption in each intervertebral region, in such a manner that the convex cartilaginous anterior extremity of one vertebra articulates with a corresponding concavity in the preceding vertebra. Thus the caducibranch Urodeles have opisthocœlous vertebrae.

Three stages can be distinguished in the development of the vertebral column of Urodeles—(1) a connection of the vertebrae by means of the intervertebrally expanded notochord, as in Fishes generally; (2) a union of the centra by means of intervertebral masses of cartilage; (3) an articular condition. An ossification of the articular surfaces of the centra of the vertebrae occurs in *Lepidosteus*, *Anura*, and most *Amniota*.

It may be noted that the articular facets appear to be the only cartilaginous portions of the vertebrae of Urodeles, their vertebrae being ossified from membrane (connective tissue), as in *Lepidosteus* and *Teleosts*. In the *Anura* the vertebrae ossify from cartilage as in the *Amniota*. The notochord persists in a cartilaginous form within the centra of the vertebrae for a long time, and may even be found in adult Frogs. The articular facets of the vertebral bodies are mostly concave in front and convex behind (procœlous) in *Anura*.

Hæmal arches are present in the tail of Urodeles, as are also transverse processes which may bear ribs. In the *Anura* the urostyle is formed by the fusion of the two anterior caudal vertebrae with the cellular sheath of the notochord.

Sauropsida.—The cellular sheath of the notochord and the neural arches from the first form a continuous structure.

In *Hatteria* and the Geckos, alone of living Reptiles, are the vertebrae biconcave, owing to the vertebral constriction of the notochord. This condition was common amongst the extinct forms. All the other *Sauropsida* agree in the sheath encroaching on the notochord in the intervertebral regions (fig. 153, D). A split occurs in the centre of each intervertebral enlargement, as in *Amphibia*, which forms the interarticular cavity. In Reptiles the articular facets of the centra are usually procœlous; they are saddle-shaped in at least the cervical region of Birds. Intervertebral discs or menisci occur between the vertebrae of Crocodiles, and, except in the cervical region, of Birds also.

Mammalia.—The view that Mammals have arisen from some group of unspecialised Reptiles receives additional support from the mode of origin of the vertebrae, as the notochord is from the first vertebraally constricted. The intervertebral regions become wholly converted into the fibro-cartilaginous menisci, intervertebral ligaments, in the centre of which the notochord persists in a degraded form as the nucleus pulposus or gelatinous pulp of

the intervertebral disc. Articular surfaces are never developed between the bodies of the vertebræ, although they occur on the neural arches. Vertebral epiphyses are peculiar to Mammals; they are found amongst Monotremes only in the caudal region, but are universally present in other Mammals, except the Sirenia.

Evolution of the Vertebral Column.—It is interesting to note that at its first appearance the foundation tissue of the skeletogenous sheath is segmented (fig. 151, *vr*), the segments corresponding with the muscle-plates; but this segmentation is soon lost.

The final segmentation of the vertebral column is alternate to that of the muscle-plates, so that the centre of each vertebra is opposite to the intermuscular septa.

As Balfour says, "The explanation of this character in the segmentation is not difficult to find. The primary segmentation of the body is that of the muscle-plates, which were present in the primitive forms in which vertebræ had not appeared. As soon, however, as the notochordal sheath was required to be strong as well as flexible, it necessarily became divided into a series of segments.

"The condition under which the lateral muscles can best cause the flexure of the vertebral column is clearly that each myotome shall be capable of acting on two vertebræ, and this condition can only be fulfilled when the myotomes are opposite the intervals between the vertebræ. For this reason, when the vertebræ became formed, their centres were opposite, not the middle of the myotomes, but the intermuscular septa."

The stages of evolution were thus—(1) the formation of axial skeletal mesoblast round the notochord by the segmented muscle-plates; (2) the fusion of these elements to form a flexible continuous sheath round the notochord and nervous axis; (3) the secondary segmentation of the vertebral column above described. The last stage consists of two phases—(a) cartilaginous, (b) osseous.

Ribs.—In most Ganoids and Teleosts the ribs arise as the cut-off extremities of the hæmal processes; in the caudal region, where the hæmal processes approach one another, the key of the arch is formed by the fused ribs. The same probably occurs in the Dipnoi.

The differentiation of the ribs is independent of that of the hæmal processes in Elasmobranchs, in which group they arise as cartilaginous bars in the connective tissue of the intermuscular septa, eventually they become connected with the hæmal processes.

The ribs appear to develop in Amphibia and Amniota much in the same way as in the Elasmobranchs, but in these groups they are attached to the neural arches or to the transverse processes.

Ribs are present in the embryos of all Amniotes throughout the vertebral column except in the tail. In the Amniota the cervical

ribs usually fuse with the transverse processes, but one or more (rarely all) may remain free. Several ribs unite to form the sternum; their ventral moities are often incompletely or entirely unossified, and constitute the sternal ribs. Behind these "true" ribs there are usually others, often termed "false," which do not reach the sternum.

In all Vertebrates the pelvis is always supported by sacral ribs; these may remain distinct, as in Urodeles, or may fuse with the transverse processes of their sacral vertebrae.

The occasional presence of abdominal parosteal splints has already been noticed (p. 193). They have been erroneously termed "abdominal ribs" by some authors.

As a matter of fact, but little is really known concerning the development of ribs, and our knowledge must be increased before it is possible to satisfactorily determine the homologies of these structures.

Sternum.—The sternum is derived from a fusion from before backwards of the ventral extremities of the ribs. The pair of cartilaginous bars thus formed fuse together to form a central plate which is later segmented off from the ribs. In Mammals especially the sternum ossifies from a series of paired centres. It is doubtful how far the so-called sternum of Amphibia is strictly homologous with the sternum of the Amniota.

Miss Lindsay has come to the conclusion that the sternum of Birds has undergone an anterior shortening, consequent upon the lengthening of the neck and the shortening of the trunk in the Avian as compared with the Reptilian type, owing to which the sternum has been severed from the ribs that formed it. The "manubrium" or "rostrum" of the Avian sternum has nothing in common with the manubrium sterni of Mammals; it is a secondary outgrowth for the attachment of the sterno-clavicular ligaments. Miss Lindsay gives the following classification of the parts of the sternum. A. Part common to Sauropsida and Mammalia: *Costal sternum* arising in two bands; connected with sternal ribs in the adult, but often losing its connection with the ribs which took part in its early formation. B. Part common to Ratitæ and Carinatae, but wanting in early embryos of the former, but never of the latter: *Metasternum*. C. Part apparently common to both Ratitæ and Carinatae, but really of different origin: *Anterior lateral process*; added to costal sternum in the Ostrich, formed by atrophy of anterior ribs in the Fowl and Gannet. D. Part absent in Ratitæ, but common to all Carinatae: *keel*; the median ventral outgrowth of B. The *posterior lateral process* is common to some Ratitæ and to most Carinatae. The *accessory processes of metasternum*, the *rostrum*, and the *xiphoid ends of posterior processes* are variable in Carinatae.

Pectoral Girdle.—Two distinct elements occur in the pectoral girdle, the one being the primitive cartilaginous element, the other consisting of superadded dermal bones (clavicles).

Without entering upon disputed details, it may be asserted in general terms that the primitive girdle consisted of a pair of laterally placed cartilaginous bars, each of which supported a pectoral fin, and which possibly arose by the fusion or extension of the basal elements of the fin itself.

In most Vertebrates the girdle is developed from such a pair of plates, which subsequently are segmented into certain pieces. Taking the articulation of the fore-limb as a starting-point, the dorsal portion is known as the scapula, and the ventral as the coracoid element. The latter is usually divisible into an anterior bar or pre-coracoid, and into a posterior coracoid proper. The girdle always becomes connected with the sternum.

Balfour found that in Elasmobranchs the girdle developed external to the muscle-plate.

The clavicles first appear in the Ganoids as large dermal scutes which have become applied to the cartilaginous girdle. In the Sturgeon there are three pairs of these scutes, the dorsal or supraclavicles, which are connected with the otic capsules of the cranium by the intervention of the post-temporal bones; the lateral elements are the clavicles, while the infraclavicles (interclavicles) meet each other in the median ventral line.

In Teleosts the dermal scutes have become subdermal bones; the interclavicles are replaced by a single median element, and postclavicles may be added. In these fishes the clavicles have, so to speak, usurped the place of the original girdle, so that while the limb is borne by the scapular and coracoid, the latter are supported by the enormously developed clavicles.

According to Götte, the interclavicles are segmented off from the ventral ends of the clavicles in Birds, and, extending between the inner edges of the two halves of the sternum, give rise when the latter unite to the keel (*crista sterni*). It is most probable that the keel is a new structure, secondarily acquired in response to the need of increased surface of attachment for the pectoral muscles. It may ossify from a single or a pair of centres. The clavicles fuse in the middle line to form the *furculum*.

In a recent paper Howes homologises the two small coracoid ossifications so constantly present in the Eutheria with the coracoid and epicoracoid of Prototheria (Monotremes), the former being the "coracoid epiphysis" and the latter the "coracoid" of human anatomists. These two elements are readily seen in the young Rabbit, which is in this respect in an intermediate condition between the Prototherian and the Eutherian type of shoulder girdle. The Mammalian "clavicles" may now be definitely regarded as ossifications around pre-existing bars of cartilage which are at first continuous with the scapulæ. The "clavicles" thus correspond with the precoracoid of Anura.

Götte has shown that the cartilaginous predecessor of the Mammalian clavicle early unites with its fellow in the median line; the tract resulting from this coalescence eventually segments into five pieces, viz., paired clavicular bars, two small nodules which represent the "lateral episterna" of Gegenbaur or the "omosterna" of Parker and a median episternum. The lateral episterna are stated by him to become attached to the clavicle or converted into the sterno-clavicular ligament. The middle piece enters into connection with the omosternum, and either becomes confluent therewith (Mole) or undergoes a retrogressive metamorphosis within its perichondrium (Lepus). Thus if the lateral bars represent, as unquestionably they appear to do, the

primary predecessors of the clavicles, this median episternum can only represent that of the interclavicle. This being so, all the elements of the Prototherian shoulder girdle are represented in that of the Eutheria.

There is so much contradiction in the accounts of the development of the clavicular elements in the Amniota that it is at present difficult to determine their precise homology.

It is possible that the "clavicles" of the Ganoids and Teleosts form a series by themselves, and that the "clavicle" of Amphibia and Amniota is merely an ossified precoracoid.

Pelvic Girdle.—The pelvic girdle arises as a pair of cartilaginous bars much in the same way as the pectoral girdle develops.

Dorsal to the articulation for the hind-limb is a single element, the ilium; but ventrally there are two elements, an anterior pubis and a posterior ischium. The space between them is known as the obturator foramen.

Locomotory Appendages.—Throughout the animal kingdom, when distinct organs for locomotion occur, apart from ciliated areas, they always develop as folds of the epiblast supported by an axial layer of mesoblast.

The epidermal surface may not be specially modified, but the mesoblast is differentiated into muscles, often numerous and complex in their action, which serve to put the appendage or limb in motion. Nerves are always, and sense-cells usually, present.

The appendages of the Craniata are always productions from the body-wall, and, being solid, never contain a diverticulum from the body-cavity; the reverse is the rule in Invertebrates. The skeletal elements of the appendages are axial in the Craniata, and, as a rule, external in Invertebrates.

Invertebrates.—The "arms" of the Starfishes are mere prolongations of the body; but owing to the reduction of the body-cavity in them, the arms of the Ophiuroidea and Crinoidea have a superficial resemblance to mere appendages. In all, the calcareous axial skeleton is of mesoblastic origin.

The parapodia of the Chætopoda are segmentally paired lateral prolongations of the body-wall, the cavity of which communicates with the body-cavity. The walls are usually greatly thickened, and normally bear setæ, and often scales, cirri, and gills. The setæ are of epiblastic origin; often a pair are immersed so deeply within each parapodium that they must serve to give a certain amount of rigidity to the structure, and thus function as a skeletal element. The parapodia may be rudimentary, and even absent (Earthworm).

The appendages of the Arthropoda are jointed tubular paired processes from the ventro-lateral aspect of each segment. The mainly chitinous exoskeleton is secreted by the epiblast; the muscles are entirely internal. The limbs at first develop as hollow buds, their cavity freely communicating with the body-cavity; but in

most cases the limb subsequently becomes solid. In several Arachnoids the alimentary canal sends prolongations into the limbs.

The larval velum and the adult locomotory organs of the Mollusca call for no special mention.

Chordata.—The locomotory appendages of the Chordata fall into two classes, the median and the paired.

Unpaired Limbs.—A median unpaired fin is characteristic of all the Ichthyopsida; in its fullest development it extends along the dorsal side of the body, commencing behind the head, passing round the tail, and, running forward along the ventral aspect of the tail, it terminates just behind the anus. The median ventral fin, however, extends in front of the anus in the adult *Amphioxus* and in embryo Teleosts.

Median Fin.—Usually the median fin is interrupted, above and below, in front of the end of the tail, so that definite regions are established which are known as the dorsal, caudal, and anal fins. The dorsal fin is frequently further subdivided.

Its development is very simple, since the fin arises as a lamellar fold of the epiblast, within which the mesoblast is modified to form muscles; and, later, fine supporting rods or fin-rays are developed, which are quite independent of the axial skeleton, although they may subsequently be closely connected with the neural and hæmal spines. The fin-rays never occur in the unpaired fin of *Amphioxus* or *Amphibia*.

The median fin is found in all larval *Amphibians*, and it is more or less developed in those adult *Urodeles* which retain an aquatic mode of life. The males of the Newt have it largely developed during the breeding season.

A dorsal fin occurs in many *Cetacea*. Here it is a fold of the skin which is supported by fibrous and fatty tissue, but without any skeletal elements. It, of course, has no connection with the dorsal fin of Fishes, but has been independently acquired.

Caudal Fin.—There can be no doubt that primitively the notochord extended as a straight tapering rod to the extreme posterior end of the animal, and that the caudal fin passed symmetrically round it. Such a protocercal or diphyccercal tail is found in *Amphioxus*, *Cyclostomi*, *Dipnoi*, and larval *Elasmobranchs*, *Ganoids*, *Teleosts*, and *Amphibia*.

The next stage in the development of the tail in *Teleosts* is characterised by the greatly increased size of the ventral lobe, resulting in the dorsal flexion of the notochord. This is the permanent condition in most *Elasmobranchs*, and is known as a heterocercal tail.

The ventral lobe projects still farther, and the dorsal portion which contains the notochord dwindles away, merely forming a kind of dorsal border to the permanent caudal fin, a condition which is characteristic of *Ganoids*.

Finally the tail becomes symmetrical externally; the fin-rays are supported by one or two greatly developed hæmal arches (hypural bones). The now ossified vertebral column apparently ends abruptly, but a rodlike bone, the urostyle, can usually be detected, which extends obliquely into the upper part of the base of the fin. The urostyle is the unsegmented ossified sheath of the upturned posterior extremity of the notochord. This is usually, but not invariably, the condition which obtains in the tails of Teleosts. The tail of the ordinary adult Teleost is, strictly speaking, as heterocercal as that of Elasmobranchs or Ganoids; but having a superficial symmetry, it is usually termed homocercal.

The protocercal nature of the larval tail is retained in Urodele Amphibia, but the notochord is replaced by the segmented vertebral column.

Paired Limbs.—Paired limbs are developed in all Craniata higher than the Cyclostomi, except in a few groups in which they have become lost.

Dohrn believes that he has found a rudiment of the pelvic fins of the Lamprey in the longitudinal folds bordering the anus and rudiments of muscles in the Ammocoete-stage.

In the Elasmobranchs, and to a less extent in Birds, the paired limbs are developed from a larval lateral ridge, which extends from behind the gill-clefts to the anus.

The ridge consists of a fold of epiblast with a core of mesoblast. It is rapidly produced into an anterior and posterior process; the intervening portion (Wolffian ridge) disappears, leaving the fore and hind pair of limbs.

In most animals the lateral ridge is not visible, each pair of limbs being apparently independent of the other. It is now generally held that the paired limbs are to be regarded as special developments of a pair of posteriorly converging lateral fins, which had essentially the same structure as the median fin.

The axial mesoblast of the limbs differentiates into cartilage, and forms the skeleton of the appendages.

Two main types of limb occur in the Craniata: the one found in Fishes is known as the ichthyopterygium; the other, peculiar to Amphibia and Amniota, is termed the cheiropterygium.

There is much controversy respecting the nature of the ichthyopterygium, based largely on speculation, but with very little positive embryological evidence; the subject is therefore quite beside the scope of this book.

The relation of the ichthyopterygium to the cheiropterygium is also at present obscure; the structure of the latter is fundamentally identical in all those animals in which it occurs. The main differences are attributable to modifications in accordance with the

habits of the animal, to the loss of certain elements, and to the fusion of parts primarily distinct.

Skull.—The skull is a composite structure, and in order to gain a clear conception of it as a whole it is necessary to bear in mind the distinctness of the parts involved. The morphology of the skull is one of the most intricate of zoological problems, consequently only the main points can be touched upon here, and these but lightly.

The old view of the segmentation of the skull, which regarded it as composed of four modified vertebræ, is now entirely abandoned, thanks to the labours of Huxley, Parker, Gegenbaur, and others. In that view the radical distinction between membrane bone and cartilage, with the bones ossified from it, was entirely overlooked, and no recourse had been made to embryology.

According to the now generally received opinion, without itself being distinctly segmented, the head corresponds to some dozen or so of the anterior segments of the body, excluding an unsegmented portion in front of the mouth, the pre-oral lobe.

The skull is essentially composed of an axial brain-box or cranium, and of three pairs of sense-capsules, and various bars which surround the mouth and visceral clefts, and which collectively form what are termed the visceral arches. To the primitive cartilaginous cranium, and the bones which may develop within it, are usually added a large number of dermal bones. For the sake of simplicity, the cranium, the visceral arches, and the dermal bones will be considered more or less separately.

In *Amphioxus* (Cephalochordata) the notochord extends in front of the neural tube; in all the Craniata the notochord terminates anteriorly immediately behind the infundibulum (fig. 94); its extremity being usually bent downwards, being probably acted upon by the cranial flexure or by the down-growth of the infundibulum.

Cranium.—A layer of mesoblast at first surrounds the brain and constitutes what is known as the membranous cranium, the notochord extending along its floor as far as the infundibulum.

A continuous tract of cartilage is next developed on each side of the notochord, hence termed parachordal; and a separate pair of bowed rods appears in front, the trabeculæ cranii. The posterior extremities of the trabeculæ embrace the apex of the notochord (fig. 155, A). The curved trabeculæ enclose a space known as the primitive pituitary space; in front they usually fuse

together below the nasal capsules. A median rod of cartilage, the prenasal rostrum, is often present between the anterior ends of the trabeculæ.

The parachordals early fuse with each other, and entirely enclose the notochord, with its skeletogenous sheath, to form the basilar plate.

The cartilaginous auditory capsule also unites with the basilar plate, which forms a ventral support for the posterior half of the brain. The notochord gradually atrophies, and, as a rule, entirely disappears.

The trabeculæ enlarge in size and fuse with the basilar plate; in the nasal region a considerable amount of cartilage is formed, and the pituitary space is reduced (fig. 155, B).



FIG. 155.—DIAGRAMS OF TWO STAGES IN THE DEVELOPMENT OF AN IDEAL CHONDROCRANIUM.

A. Early stage, with the trabeculæ and parachordals as simple bars and membranous sense capsules. B. Later stage, in which a fusion of the above elements has occurred and the cartilaginous nasal and auditory capsules are incorporated in the cranium. C. Side view of about same stage as B.
a.o. antorbital process; *au.* auditory capsule; *br.* branchial arches; *c.* cornua trabeculæ; *hy.* hyoid arch; *mn.* Meckel's cartilage, mandibular arch; *na.* nasal capsule; *na.ar.* neural arch; *nch.* notochord; *op.* optic capsule; *p.ch.* parachordal; *pl.pt.* palato-ptyergoid arch; *p.o.* post-orbital process; *p.s.* pituitary space; *q.* quadrate; *r.* rostrum; *tr.* trabeculæ.

The nasal capsule is supported anteriorly by the outwardly curved extremities of the trabeculæ, the cornua trabeculæ; and posteriorly by a spur of cartilage, the preorbital process. Thus, like the auditory capsule, the nasal capsule is early engrafted into the cranium. The optic capsules or eyeballs always remain free.

The floor of the cranium being thus laid, the walls are raised by vertical upgrowths from the sides of the basal cartilage. Between the auditory capsules the walls usually meet above the brain and form the posterior cranial roof; and a solid upgrowth of cartilage often occurs anteriorly between the nasal capsules.

The primitive cartilaginous cranium (chondro-cranium) thus consists of a ventral plate and lateral walls of cartilage, which enclose the auditory and olfactory capsules, and a posterior roof. The

floor is perforated by the pituitary space, through which also the internal carotid artery at first passes. The cranial nerves pass through apertures (foramina) left during the extension of the cartilage.

Definite regions can be made out in the chondro-cranium at this stage, which may now be enumerated.

The posterior roofed extremity of the skull, occipital region, articulates with the anterior vertebra (except in Cyclostomes, some Elasmobranchs, Ganoids (except *Lepidosteus*), and Dipnoids, in which forms the persistent notochord is continued into the skull, or the occipital region is fused with more or fewer of the anterior vertebrae. In front of the occipital is the auditory region, and between them is the aperture (foramen lacerum posterius) for the glosso-pharyngeal (IX.) and vagus (X.) nerves (fig. 156).

The sphenoidal region extends from the auditory to the nasal capsule; an anterior and posterior pair of cartilages usually grow up from the basi-sphenoidal cartilage, which are respectively known as the orbito- and ali-sphenoid plates. A large slit-like orifice (foramen lacerum medius) is left between the auditory capsule and the ali-sphenoid; in it is lodged the Gasserian ganglion, and through it emerges the trigeminal (V.) nerve. Between the ali- and orbito-sphenoid is a cleft (foramen lacerum anterius or sphenoidal fissure) through which the optic nerve (II.) and the motor nerves of the eyeball (III., IV., VI.) pass; the fourth nerve sometimes passes out independently above the optic foramen. The cartilage at the base of the ali-sphenoids (basi-sphenoid) is continuous with that below the orbito-sphenoids (pre-sphenoid).

Between the nasal capsules is the ethmoid region.

Such a chondro-cranium as that described above is practically the permanent condition of the crania of all Fishes, except the Teleosts and bony Ganoids. In the Ganoids ossification commences in more or fewer of these cartilaginous areas, and, with some variation, the bones which result from these centres of ossification occur all through the Vertebrate series.

It not unfrequently happens that cartilage extends beyond its primitive area and encroaches on other regions or surrounds certain nerves or blood-vessels, or two or more ossifying tracts may fuse to form a compound bone. On the other hand, portions of the chondro-cranium may atrophy, or even not be developed at all.

Visceral Arches.—Cartilaginous bars are early developed in the lateral walls of the pharynx between the visceral clefts. These

visceral arches, as they are termed, are primitively very similar, and each consists of a simple bar of cartilage, which later may become segmented, and usually more or less ossified. The greatest number occurring in any animal are found in the Cyclostomi and Notidanus, where there are nine in all: as a rule, there are seven in the Ichthyopsida and fewer in the Amniota.

The first is the mandibular arch, the second is the hyoid, and the remainder are known as branchials.

It was formerly thought that the branchial basket-work of the Cyclostomi belonged to a different series of cartilages from the visceral arches of Gnathostomatous Crani-

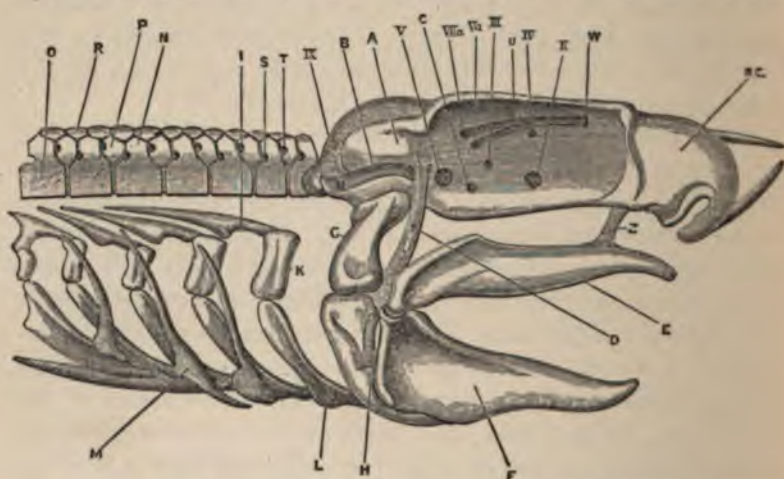


FIG. 155.—THE CHONDRO-CRANIUM AND VISCERAL SKELETON WITH THE ANTERIOR PART OF THE VERTEBRAL COLUMN OF A DOG-FISH (*Scyllium canicula*). Seen from the right side; the labial cartilages are omitted. [After A. M. Marshall.]

A. auditory capsule; B. post-orbital groove; C. inter-orbital canal; D. pre-spiracular (meta-ptyergoid) ligament, with the pre-spiracular cartilage; E. upper jaw (pterygoquadrate arcade); F. lower jaw (Meckel's cartilage); G. hyo-mandibular cartilage; H. cerato-hyal; I. pharyngo-branchial; K. epi-branchial; L. cerato-branchial; M. extra-branchial; N. vertebral neural arch; O. olfactory capsule; P. centrum of vertebra; Q. intervertebral neural arch; R. neural spine; S. foramen for the ventral root of a spinal nerve; T. foramen for the dorsal root of the preceding nerve; U. orbital groove, lodging the ophthalmic branches of the fifth and seventh nerves; V. aperture at end of orbital groove through which the above-mentioned branches leave the orbit; W. ethmo-palatine (palato-trabecular) ligament; X. optic foramen; Y. foramen for third nerve; Z. foramen for fourth nerve; AA. foramen for the main branches of the fifth and seventh nerves and for the sixth nerve; AB. foramen for the ophthalmic branch of the fifth nerve; AC. foramen for the ophthalmic branch of the seventh nerve; AD. foramen for the ninth or glossopharyngeal nerve.

ates, the former being supposed to be developed on the outer wall of the so-called head-cavities, while the latter arose from their inner wall. The extra-branchial cartilages of Elasmobranchs (fig. 156) were also supposed to be rudiments of the external series. Dohrn has, however, shown that there is no real distinction between these elements, and that the branchial skeleton of Lampreys is as truly internal as that of other Craniates, the main distinction being that in Cyclostomes the visceral arches are unsegmented. Dohrn also finds that the extra-branchials of Elasmobranchs are merely the dorsal and ventral cartilaginous branchial rays of their respective arches, which early shift their position.

Mandibular Arch.—From the mandibular arch a bud grows forward on each side in front of the mouth, and a separation occurs in the arch at the angle of the mouth, so that an upper and a lower jaw cartilage result, which articulate together. The upper jaw arch is termed the palato-quadrate or pterygo-quadrate arcade; the lower bar forms Meckel's cartilage. The portion of the primitive arch above the pterygoid bud is the metapterygoid, and possibly constitutes the primitive means of attachment of the jaw with the cranium.

The mandibular arch may posteriorly be supported solely by the proximal element of the hyoid arch (hyomandibular), or partially by the latter and partly by its own proximal portion (metapterygoid?), or the mandibular arch is directly attached to the cranium without the intervention of the hyoid arch. The first mode of attachment, known as hyostylic, occurs in many Elasmobranchs, and in most Ganoids and Teleosts; the second or amphistylic is found in the Notidanidæ and Cestracion; the last, autostylic, is peculiar to Holocephali, Dipnoi, Amphibia, and Amniota.

The upper jaw arch may anteriorly be quite independent of the cranium, or attached by a ligament ethmo-palatine or palato-trabecular ligament, or by a cartilaginous bar, the palatine. In the Holocephali and Dipnoi the whole of the pterygo-quadrate bar is fused with the base of the cranium.

The quadrate, or that region on which the lower jaw articulates, is usually cut off as a distinct element, and serves, in the Sauropsida, as the support (suspensorium) for the mandible. In Mammals it is pressed into the service of the internal ear as the incus (p. 151).

In the cartilaginous Fishes, Meckel's cartilage, or the primitive cartilage of the lower jaw, is very massive; but in other forms, although always present in early life, its place is generally usurped by membrane bones.

The proximal articulating element is segmented off in Mammals, and now generally regarded as the malleus.

Ossifications occur in certain centres of the cartilage, or in the perichondrium, but the details of these ossifications in this and the succeeding visceral arches do not fall within the scope of this book.

Hyoid Arch.—The upper portion of the hyoid arch segments off in Fishes as a distinct cartilage, the hyomandibular, to which allusion has just been made. The inferior moiety becomes divided into several rod-like pieces, which may become ossified.

From his researches on the development of Fishes, Dohrn finds that the problem of the original number of visceral clefts and arches is not so simple as is generally imagined. He is satisfied that what is usually regarded as the hyoid arch is certainly a double structure. He also regards the spiracular cartilage as being the rudiment of another arch, and he is inclined to believe that both the upper and the lower jaws are cartilages belonging to distinct arches. According to him, the enumeration of the visceral arches of the jaw and hyoid regions would be: 1. upper jaw; 2. lower jaw; 3. spiracular cartilage; 4. hyomandibular; 5. hyoid. The clefts between the mandibular and hyoid arches have become difficult to recognise as such; the median thyroid body may perhaps represent the coalesced rudiments of one pair.

Branchial Arches.—The greatest number of branchial arches obtains in *Heptanchus*, *Notidanus*; where there are seven, in most Fish there are five (fig. 156); this number may be considerably reduced in Teleosts. The originally continuous bars become jointed, and may ossify.

Basi-hyoid and basi-branchial cartilages are universally present. A cartilage which Huxley believes may represent a basi-mandibular element is present in the *Cyclostomi*.

In the adults of the *Caducibranchiate* Amphibia and Amniota the post-oral visceral skeleton is greatly reduced, and is represented by the so-called "hyoid." In reality this composite structure consists of a flat plate or body, which results from the fusion of the median pieces of the hyoid and first branchial arch. The anterior or greater cornua are the persistent hyoid arches, and the posterior or lesser cornua are the degenerate first branchials. What appears to be a vestige of the second branchial arch has been described by Howes for *Phocæna*, and several branchial elements enter into the "hyoid" in most Amphibia.

Dermal Bones.—The chondro-cranium of Elasmobranchs is simply covered by the skin of the head. In Ganoids the brain is further protected by large bony plates, which assume a more or less regular disposition. Certain of these plates persist in Teleosts as the dermal bones of the skull, and similar bones with an analogous distribution are found in higher animals.

An irregular median series is sometimes present, but these are crowded out by a paired series, which form the roof-bones of the skull.

Membrane bones are developed on the side of the face, along the upper and lower jaw, on the roof of the mouth, and outside the hyoid arch.

Those parosteal bones (ex. parasphenoid, vomers), which are developed within, or in some cases at the side of the mouth, appear to be primarily due to the fusion of the basal portion of teeth.

All the above elements collectively constitute the skull.

Body-Cavity.—The mode of formation of the body-cavity is necessarily dependent upon the development of the mesoblast, and has already been incidentally dealt with; there is, therefore, no need to repeat the former descriptions or inferences.

It is necessary to remember that, with the exception of the lower Worms and Molluscs, diverticula or pouches (somites) grow out from the archenteron and become separated from it. The sacs thus formed increase in size and surround the alimentary canal. Their outer wall (somatic mesoblast) becomes applied to the epiblast to form the body-wall (somatopleur) and their inner wall (splanchnic mesoblast) together with the hypoblast constitutes the somatopleur; their cavity is the *cœlom* or true body-cavity.

The mesothelium which forms the walls of the somites may differentiate into various structures, but it nearly always gives rise to a delicate epithelium (peritoneum or serous membrane) on the surface facing the body-cavity. The somatic epithelium is known as the parietal layer, the splanchnic as the visceral layer of the peritoneum.

As the visceral or splanchnic walls of each pair of somites approach one another they form a double-layered membrane, the mesentery. In some animals the primitive dorsal and ventral mesentery may persist, but usually the mesentery is largely absorbed leaving strands of tissue (mesenteries) which sling the alimentary canal.

In *Cyclops*, according to Urbanovics, the body-cavity is formed by a fusion of paired excavations of a mesoblastic band; the dissepiments between only disappear very late. The dorsal and ventral mesenteries persist; the dorsal mesentery contains a space which is a remnant of the blastocœl, and plays an important part in the circulation in the absence of the heart. It is difficult to understand why this should not be regarded as a true heart; it may be a rudimentary structure, but the development is similar to that of a heart (p. 215).

The behaviour of the somites in *Amphioxus* gives us a key to the original mode of formation of the body-cavity in the Chordata. The segmented somites are developed from the dorso-lateral angles of the archenteron (fig. 56); subsequently they extend ventrally forming the somatic and splanchnic mesoblast, finally the upper portion loses its central cavity and becomes converted into the lateral muscles of the body, which always retain their original segmentation. The ventral portions of the somites not only fuse with their fellows, but form a continuous body-cavity which extends along the whole length of the body.

In all Chordata the primitive segmentation of the body is retained solely by the dorsal moieties of the somites—primarily in the muscles, secondarily in the vertebral column, and partially in the excretory organ. The two former are developed from the main portion of the dorsal halves of the somites, which eventually are entirely separated from the ventral halves. Before this is effected they are connected by what is known as the "intermediate cell mass" (figs. 150, 174, 178*). This tissue gives rise to the excretory organ (p. 243).

At the origin of the mesentery, the peritoneum is columnar throughout a considerable length of the body-cavity, and constitutes the germinal epithelium (fig. 175, *p.o.*).

Mesentery.—As the alimentary canal of Vertebrates is at first a simple straight tube, so the mesentery which slings it forms a simple fold. With the appearance of distinct regions in the alimentary canal, those portions of the mesentery which suspend them receive corresponding names; thus the mesogastrium, the mesocolon, and the mesorectum.

In Man the stomach is at first an antero-posterior dilation of the mesenteron, as is permanently the case in most of the lower Vertebrates. The stomach soon turns over towards the right side, so that the mesogastric border is turned to the left, but the stomach still retains its longitudinal direction, as in some adult Mammals. The new left border bulges out to form the greater curvature, and the stomach assumes by degrees a transverse direction, carrying the mesogastrium with it. As a result of this rotation of the stomach, a mesogastric sac is formed which is the commencement of the omentum; the orifice of the sac is the foramen of Winslow. The omentum increases in size and extends down to the colon.

In Fishes the kidneys remain above the dorsal wall of the body-cavity; in Amphibia and higher forms they project slightly into the cœlom, being more or less suspended by folds of the peritoneum.

The generative glands are suspended within distinct folds of the peritoneum, which are known as the mesorchium for the testis, and mesoarrium for the ovary.

It must be borne in mind that the viscera which are described as lying within the body-cavity are all, morphologically speaking, outside it. The body-cavity or cœlom is a closed sac lined by a serous membrane. Various viscera may sink into the contained cavity, but they always push before them the serous membrane, which thus forms a fold round them. All structures such as blood-vessels or nerves pass to and from the viscus between the laminae of the fold of the serous membrane.

Pericardium.--The anterior portion of the primitive body-cavity undergoes certain changes. A horizontal septum is formed, connecting the splanchnopleur with the somatopleur of each side on a level with the ductus Cuvieri at the spot where they enter the sinus venosus, and really serving to support these vessels.

The transverse septum extends anteriorly and posteriorly; below lies the heart, and above is the alimentary canal. As the septum stretches from the body-wall to what may be termed the dorsal mesocardium (fig. 159), it naturally divides the anterior region of the body-cavity into a ventral pericardium and a pair of dorso-lateral cavities; these all communicate anteriorly and posteriorly. By further growth forwards of the septum, the pericardium is cut off from the anterior dorsal horns of the body-cavity. The septum extends posteriorly along the under side of the liver till it reaches the ventral wall of the body, where the liver is attached by its ventral mesentery (falciform ligament); but a posterior canal, usually opening into the general body-cavity by two orifices, persists in Elasmobranchs.

The pericardium is thus a specialised portion of the body-cavity, and therefore it is lined by its serous membrane, which was primitively continuous with that of the coelom. As its viscus, the heart, depends into the pericardial cavity in the same manner as the mesenteron depends into the body-cavity, so it is covered by the reflected or visceral portion of the pericardium, the outer being known as the parietal portion.

In air-breathers the developing lungs project on each side of the throat into the dorso-lateral extensions of the body-cavity above the pericardium. This condition is practically retained in Amphibia and most Reptiles. The common body-cavity is thus often termed in them the pleuro-peritoneal cavity.

Diaphragm.--The diaphragm later makes its appearance by a dorsal extension of the posterior wall of the pericardium, which cuts off the pleural-cavities from the abdominal coelom. The diaphragm is at first tendinous; the muscle grows in later from the dorsal side, probably from the muscle-plates.

Uskew enumerates the following grades of development:--

1. The ventral and dorsal portions of the diaphragm are fully developed; they completely divide the coelom, and have muscles. The diaphragm is entirely separated from the pericardium, except two thin lamellæ (Rabbit).
2. Similar, but a part of the diaphragm remains united with the pericardium (Man).
3. Same as 2, but the diaphragm contains no muscles, and its ventral part is completely fused with the pericardium (Fowl).
4. Similar to 3, but the dorsal part is not completely developed, remaining in a primitive condition (Lizard) or in an early stage (Frog).
5. Like 4, the diaphragm is not separated from the pericardium, persisting at the stage of the septum transversum (Myxinoids and *Ammocete*).
6. The Teleosts form a distinct type; although, as in the Salmon, there is a certain separation of the diaphragm from the pericardium, even more than in Birds, yet the dorsal portion is completely wanting.

Pleurae.--The serous membrane of the pleural cavities is termed the pleura, and, as in the case of the pericardium, a parietal layer (costal pleura) and a visceral layer (pulmonary pleura) are present. The mediastinal space is that space which occurs between the closed pulmonary serous sacs, the mediastinum itself being formed by the junction of the parietal pleura of each side.

In the adult males of the higher Euthera the primitive coelom is divided into the following perfectly distinct serous sacs:--The two pleurae and the pericardium, which together form the thoracic cavity, the abdominal cavity, and the paired tunica vaginalis (p. 262).

Abdominal Pores.--A pair of apertures, by means of which the abdominal cavity is placed in direct communication with the

exterior, occurs in Cyclostomi, Elasmobranchii, Ganoidei, a few Teleostei, Dipnoi, Chelonia, and Crocodilia. Occasionally there is only a single pore.

These abdominal pores, as they are termed, usually open into the cloaca on each side of the urogenital aperture, but they may occur outside the cloaca, and either in front or behind.

In Cyclostomes, Scott states they are developed from the hypoblastic section of the cloaca; in other forms they arise as epiblastic pits, but the pores in Cyclostomes may not be homologous with those of other animals. The abdominal pores of most Teleosts have also been regarded as not homologous with those of other fish (see p. 258).

They serve for the egress of the generative products in Cyclostomes and a few Teleosts.

Abdominal pores are entirely absent in Amphibia and Birds, and have not been recognised in Mammals. It is, however, possible that the inguinal canals of Mammals, which have a similar relation to the urogenital orifice, may prove to be remnants of the abdominal pores of their hypotherian ancestors.

The branchial or atrial pore of *Amphioxus* is often erroneously termed an abdominal pore; its mode of formation (p. 178) proves these two pores have nothing in common.

The Vascular System.—The vascular system consists of a closed network of vessels containing a fluid (plasma), within which float free cells (blood corpuscles). The whole is invariably derived from the mesoblast.

There are yet numerous gaps in our knowledge of the development of blood-vessels in various animals. Two modes of formation have been described for both Invertebrates and Chordata.

Development of Blood-Vessels.—In the vascular area of the blastoderm of Amniotes, the mesoblast cells form a protoplasmic network. Some of the nuclei of these cells rapidly divide and form masses of nuclei. The protoplasm round each nucleus acquires a red colour (hæmoglobin), and, on the deliquescence of the central portion of the protoplasmic network become liberated as red-blood corpuscles. The peripheral nuclei form the nuclei of the walls of the vessels.

A similar mode of formation of blood-vessels has been described by Lankester in the adult Leech, and it is probably of wide occurrence.

The process may be summed up as a liquid vacuolation of certain reticular mesoblastic tissue. Some of the nuclei remain in the walls of the channels, others (red blood-corpuscles) with free mesoblastic elements (white blood-corpuscles) are suspended in

the fluid (plasma) thus formed, and, on the assumption of contractility by the walls of the main vessels, they are hurried along in the general circulation.

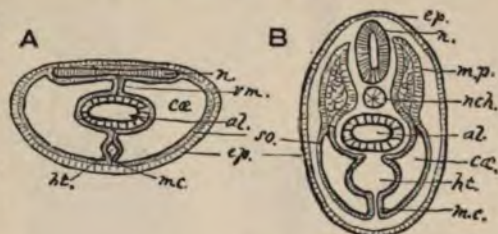
The second mode of vascular development consists in linear masses of mesoblast cells being formed, the outermost of which arrange themselves into a tube containing the central free cells or corpuscles. This occurs in the trunk of Vertebrate embryos, and is usually described for Invertebrates generally.

In the lower Invertebrates the vascular system is either not at all or very imperfectly developed. The Chætopod Worms have a large dorsal (abneural) blood-vessel, which is very contractile and drives the blood from behind forwards; some of the lateral branches are also contractile. The Mollusca and Arthropoda possess a distinct heart, which in the latter may be considered as a concentration of the elongated dorsal vessel of the higher worms.

Although many of the blood-vessels in Amphioxus are contrac-

FIG. 157.—DIAGRAMS ILLUSTRATING THE FORMATION OF THE HEART OF (A) INVERTEBRATES AND (B) CHORDATA.

The neural aspects are placed the same way in both diagrams to facilitate comparisons.
al. mesenteron; *co.* coelom or body-cavity; *ep.* epidermis; *ht.* cavity of heart; *mc.* mesocardium; *m.p.* muscle-plate; *n.* central nervous system; *not.* notochord; *so.* peritoneum (somatic mesoblast); *v.m.* ventral mesentery (of Invertebrates).



tile, no distinct heart is present. In the true Vertebrates a heart is always present, and the blood-vessels retain their contractibility to a greater or less extent.

Formation of the Heart.—The origin of the heart in many Invertebrates is still a matter of some uncertainty. From the recent investigations of Bütschli, Schimkewitsch, and others, it would appear that the cavity of the heart, at least in certain of the Annelida and Arthropoda, is a persistent portion of the segmentation-cavity which has been enclosed between the vertical walls of the archenteric diverticula where they join one another to form the dorsal (abneural) mesentery (fig. 157, A).

Patten, on the other hand, maintains that although in the Cockroach (*Blatta*) the heart is formed by the junction of the two folds of mesoblast, the cavity of the heart is not the space included between the two folds, but is in reality an enclosed portion of the true body-cavity. The folds of the mesoblast pulsate long before a special heart is formed, and a circulation occurs through the irregular sinuses of the body-cavity. Blood corpuscles arise before the formation of the heart by the liberation of indifferent cells, and afterwards from the walls of the heart itself.

In the Spider [Balfour, but not Schimkewitsch] and in some of the higher Crustacea (Asellus [Dohrn], Astacus and Palæmon



FIG. 153.—TRANSVERSE SECTION THROUGH THE HEAD OF A RABBIT OF EIGHT DAYS FOURTEEN HOURS. [From Kölliker.]

A. Magnified 48 diameters.—*h*, *h*, paired rudiment of heart; *sr*, cavity of mesenteron.
B. Part of A magnified 152 diameters.—*ahh*, muscular wall of heart; *dd*, hypoblast; *dd*, thickening of hypoblast to form the notochord; *dip*, splanchnic mesoblast; *h*, epiblast; *hp*, somatic mesoblast; *ahh*, epithelioid layer (endothelium) of heart; *mes*, lateral undivided mesoblast; *mp*, neural plate; *ph*, pericardial section of body-cavity; *rf*, neural groove; *sw*, neural fold; *sp*, intermediate cell-mass; *sw*, part of the hypoblast which will form the ventral wall of the pharynx.

[Bobretzky]) the heart is said to arise from a solid rod of mesoblast cells, of which the central portion becomes the corpuscles. This may, however, prove to be only a secondary mode of formation.

The formation of the heart in Vertebrata appears to be essentially identical with that in Invertebrates, the cavity of the heart being that space which is left between the median walls of the lateral halves of the body-cavity as they approach one another below the throat (fig. 157, B).

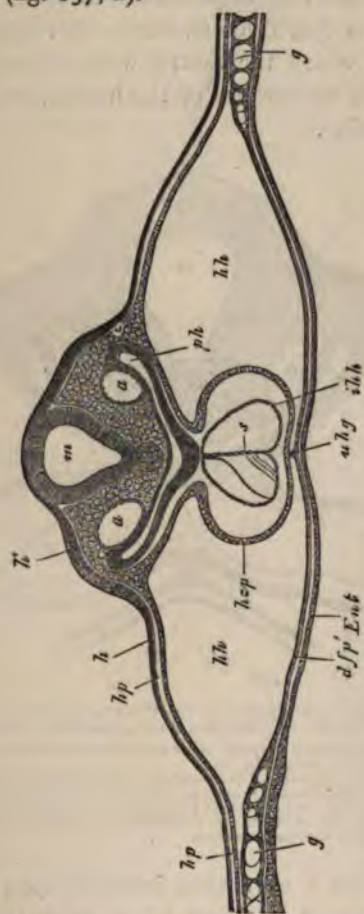


FIG. 159.—TRANSVERSE SECTION THROUGH THE CARDIAC REGION OF AN EMBRYO FOWL OF THIRTY-NINE HOURS. Magnified 61 diameters. [From Kölliker.]

a, aortic arches; *d/p'*, somatic mesoblast of throat; *Ent*, epiblast of wall of throat; *g*, vessels of the internal border of the area opaca; *h*, epiblast; *AA*, body-cavity of neck; *hp*, dorsal somatic mesoblast; *hsp*, muscular wall of heart; *thh*, endothelium of heart; *m*, neural canal; *ph*, pharynx; *s*, septum formed by the junction of the two endothelial tubes; *uhg*, inferior cardiac mesentery (mesocardium) formed by the meeting of the splanchnopleur below the developing heart; the corresponding though widely separated folds between the heart and the pharynx may be termed the dorsal, and the former the ventral, mesocardium.

Shipley has very recently shown that the heart of the embryo Lamprey develops in the same manner, the endothelium being derived by the splitting of the approaching walls of the splanchnopleur. The blood-corpuscles originate from the free edges of the lateral plates of mesoblast.

As Balfour has shown, the heart will from the first appear as single or double, according to the relative time of its formation.

In Elasmobranchs and Amphibia the throat early becomes constricted off from the yolk, and in these groups the heart appears as a single tube in the ventral (abneural) mesentery (mesocardium); but in those forms (ex. Teleosts, Birds, figs. 159, 160, and Mammals, fig. 158) in which the ventral wall of the throat is formed later than the first appearance of the heart, the latter necessarily develops as two tubes.

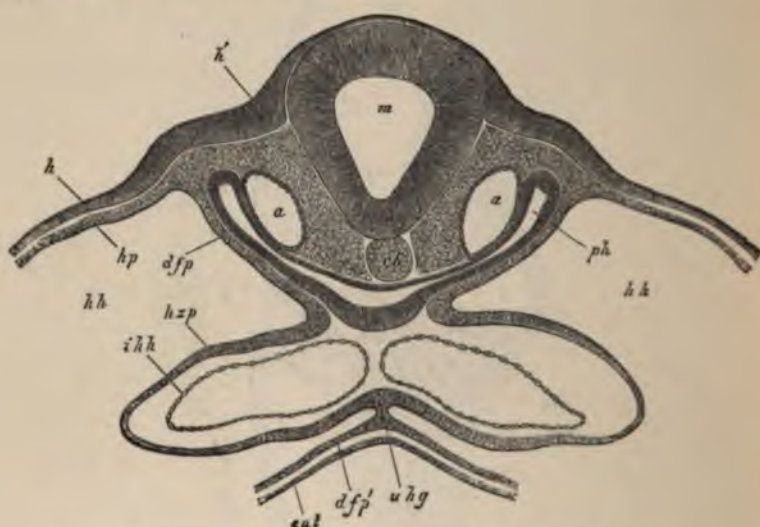


FIG. 160.—TRANSVERSE SECTION THROUGH THE CARDIAC REGION OF AN EMBRYO FOWL OF THIRTY-NINE HOURS. Magnified about 95 diameters. [From Kölliker.]

The section passes through the point where the omphalo-mesenteric veins open into the heart, and therefore behind fig. 159.
a, aortic arch; *ch*, notochord; *d/p*, splanchnic mesoblast; *d/p'*, somatic mesoblast of throat; *ent*, epiblast of wall of throat; *h*, epiblast; *h'*, thickened portion of epiblast where the auditory sacs will be formed; *h h*, body-cavity of neck; *hp*, somatic mesoblast; *asp*, muscular wall of heart; *i h h*, endothelium of heart; *m*, neural canal; *ph*, pharynx; *u h g*, inferior cardine mesentery.

The Fowl occupies a somewhat intermediate position, since the extreme anterior end of its heart arises as an almost single tube; but it diverges posteriorly, each limb of the Λ thus formed being one of the veins which bring the blood back from the yolk (vitelline veins) (fig. 161).

The internal epithelium (endothelium) of the heart is single or double like the heart itself; but when the two tubes unite to form the single heart, the endothelial tubes also coalesce; but just at first there is a median septum left (fig. 159, *s*), indicating where the two tubes have joined; this soon breaks through, and a single

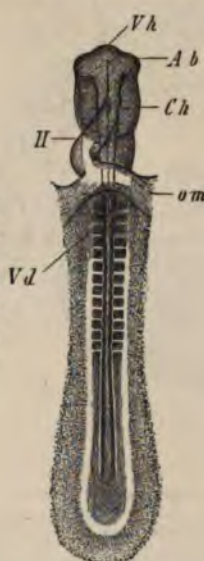
tube results, the thick walls of which early become very muscular.

It follows from what has been stated concerning the mode of development of the Fowl's heart, that at an early stage an anterior section would show the imperfect coalescence of the lateral endothelial tubes, whereas one taken a little farther behind would only exhibit the approximation of these tubes. Thus in the same embryo several stages in the development of the heart would be illustrated. The anterior section would be the most advanced, and the approaching vitelline veins would represent a much earlier period (see figs. 159-160).

The primitively straight tubular heart of the Chordata undergoes

FIG. 161.—VENTRAL VIEW OF EMBRYO FOWL AT THE END OF THE SECOND DAY. 4.27 mm. long; removed from the blastoderm. [From Kolliker.]

Ab. optic vesicle; *Ch.* notochord; *H.* heart; *om.* omphalo-mesenteric or vitelline vein; *Vd.* indicates the backward extension of the head-fold: in front of this point the pharynx is inferiorly completed; while behind, the alimentary tract is still open below to the yolk.



a sigmoid flexure, at first slight (fig. 161, H), but eventually the S-like flexure is complete (fig. 162, 3). The dorsal limb constitutes the auricular portion (atrium), and the ventral forms the ventricular part. The dorsal and ventral portions are separated by a constriction.

There is present in Fishes in connection with the atrium a posterior thin-walled sac, the sinus venosus, into which the collecting veins (ductus Cuvieri) open, and into the single auricle. A pair of valves guard the orifice leading to the ventricle.

The posterior region of the ventricular moiety becomes the ventricle of the adult, while the anterior portion is divided into a

posterior conus arteriosus and an anterior bulbus arteriosus. The conus is long, and provided with several transverse rows of valves, except in most Teleosts, in which group it is rudimentary or absent. The non-valvular bulbus leads to the branchial arteries.

Among the Dipnoi the blood-vessel bringing blood from the air-bladder (lungs) to the heart opens into a small second (left) auricle. The conus and ventricle may also be partially divided in two by an imperfect longitudinal septum.

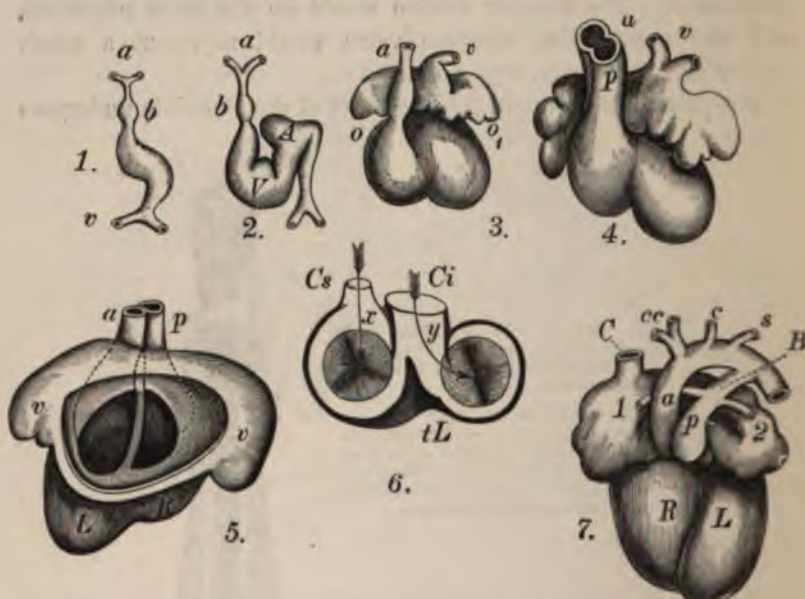


FIG. 162.—DEVELOPMENT OF THE MAMMALIAN HEART. [From Landolt and Stirling.]

1. Heart with slight curvature. 2. Sigmoid flexure of the heart. 3. Formation of the auricular appendages, and external furrow in the ventricle. 4. Commencing division of the truncus arteriosus. 5. Dorsal view; the auricle has been opened to show the ventricular septum; the aorta (a) and pulmonary artery open into their respective ventricles. 6. Diagrammatic view from above of the mode in which veins came open into the auricle. 7. Ventral view of heart of full-time fetus.

A, auricular portion of heart; a, aorta; B, ductus arteriosus Botalli; b, bulbus arteriosus; c, carotid; c.c. innominate; Ci, inferior vena cava; Cs, superior vena cava; L, left ventricle; o. o. i. auricular appendages; p, pulmonary artery; R, right ventricle; s, left subclavian artery; V, ventricular portion of heart; v, auricle and veins entering the heart; x, arrow showing the flow of blood from the superior vena cava through the valve into the right auricle, and y that of the inferior vena cava through the valve into the left auricle; 1 and 2, right and left pulmonary arteries.

The single auricle of the primitively piscine heart of the Amphibia is early provided with a pair of lateral appendages, and an oblique septum is developed which divides the single auricle (atrium) into a right and left chamber. The ventricle remains single; the conus arteriosus (pylangium) has a longitudinal valve and a row of valves at each end; there is also a bulbus arteriosus (synangium), which, however, is rudimentary in the

Anura. The conus and bulbus are usually collectively known as the truncus arteriosus. A sinus venosus is also present.

The flexure of the developing heart is very marked in the Amniota. The auricular portion develops lateral appendages; the large venous trunk which opens into this region (fig. 162, 3, *v*) is composed of the superior and inferior venæ cavæ. This common trunk is later absorbed into the enlarging auricle, and thus arises the separate termination of these vessels (fig. 162, 4, *v*). The constriction between the auricular and ventricular divisions of the heart is known as the canalis auricularis.

The heart begins to divide into a right and left half on the third day in the Fowl and about the fourth week in Man, the division first occurring in the ventricle. The ventricular septum arises from the ventral wall and rapidly extends to the dorsal, dividing

FIG. 161.—LATERAL VIEW OF HEART OF HUMAN EMBRYO, THE RIGHT SIDE BEING CUT AWAY. [After Hiss.]

a, aortic channel; c.c. coronary vein; d, diaphragm; l, liver; p, pulmonary channel; s.a, septum aorticum in the bulbus aorta; s.inf, septum inferius; s.int, septum intermedium; s.r, sinus reuniens; s.s, septum superius; v.c.i, vena cava inferior; v.c.s.l, vena cava superior (left); v.c.s.r, vena cava superior (right); v.e, Eustachian valve.



the ventricle into two somewhat curved chambers, one more to the left and above, the other to the right and below. Thus the large undivided auricle communicates by a right and left auriculo-ventricular opening with the corresponding ventricle (fig. 162, 5).

A fold appears on the ventral wall of the auricle, dividing the cavity into a right and left chamber. The fold extends only a short distance, thus forming an incomplete septum (the auricular septum). The right and left auricles communicate throughout embryonic life by means of the aperture thus left, the foramen ovale (fig. 163).

The vena cava inferior opens into the right auricle directly opposite the auricular septum, and its blood has a tendency to flow through the foramen ovale into the left auricle. The right vena cava superior joins the vena cava inferior, and its blood also passes into the left auricle. The left vena cava superior opens

independently into the right auricle, and its blood flows into the right ventricle.

A valve, the Eustachian valve, next develops from the dorsal wall of the right auricle to the right of the entrance of the vena cava inferior into the auricle, and between it and the right and left superior venæ cavæ. This serves to still further direct the blood from the vena cava inferior into the left auricle, and at the same time to retain the blood of the superior venæ cavæ within the right side of the heart. In many of the higher Mammals, including Man, the right vena cava superior disappears during foetal life.

A second fold arises from the dorsal wall in the median line of the auricles; this projects freely across, and to the left side of, the foramen ovale, thus forming a valve which prevents the blood from flowing back from the left to the right auricle.

The left auricle is at first larger than the right. Later the cavities approximate in size, and the foramen ovale is much smaller.

Lastly, the truncus arteriosus is longitudinally divided in Birds by a septum, which arises between the fourth and fifth pair of arches and extends in a somewhat spiral manner to close to the ventricular orifice. In Mammals the truncus (fig. 162, 4, *ap*) appears to be constricted dorsally and ventrally to form the aorta and pulmonary artery.

Semilunar valves are developed in the short interspace between the orifice and the free end of the septum of the truncus. The dorsal and ventral valves first appear, the former as a continuous ridge, the latter as a pair of small processes. The septum of the truncus extends between the latter, and, entirely dividing the ventricular orifice, fuses with the ventricular septum.

By the division of the truncus in Birds, the fifth pair of arches communicates with the right ventricle, while the third and fourth pairs communicate with the left ventricle; of these, the former becomes the pulmonary arteries, and the two latter the carotid and aortic arches respectively (p. 227). In Mammals, also, the right ventricle is continuous with the last aortic arch, the four anterior arches, or what remains of them, being connected with the left ventricle.

In all Reptiles, except the Crocodiles, the primitively single ventricle is retained. The ventricular septum was independently acquired by Crocodiles, Birds, and Mammals; thus in these three groups it is what is termed homoplastic, but not

homogenetic. An interesting example of the "falsification of the embryological record" is afforded, as Bell points out, by the development (ontogeny) of the ventricles, as in those forms in which they become distinct the ventricular septum develops prior to the auricular septum, whereas in the true phylogeny the reverse occurred. This is a case of what Haeckel calls cenogeny, and is no doubt dependent on the requirements of the organism.

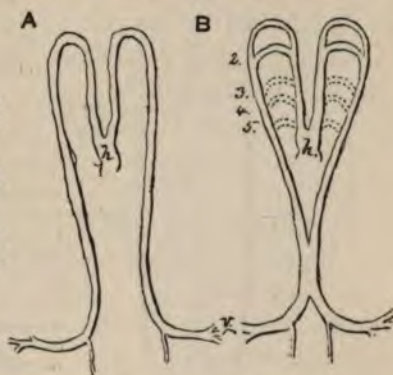
The complicated series of changes undergone in the evolution of the Vertebrate heart is apparently mainly the result of the modifications which have occurred in the respiratory organs. Without going into details, the following facts are worthy of note:—The respiratory tract of *Amphioxus* is extremely long, the "heart" is undifferentiated, and the median ventral vessel (subintestinal vein) is contractile; in Fishes the pharynx is much shorter, and is increasingly reduced in the more specialised forms; the flexure of the heart may be related to the shortening of the neck; the assumption of aerial respiration by the air-bladder, and a change in the origin of its afferent, and in the destination of its efferent blood-vessels; the necessity for the brain and sense-organs being supplied with well-oxygenated blood.

Development of the Vascular System in Vertebrates.—
In the following brief account of the evolution of the vascular

FIG. 164.—DIAGRAMMATIC OUTLINES OF THE EARLY ARTERIAL SYSTEM OF A MAMMAL VERTEBRATE EMBRYO. [After Allen Thomson.]

A. At a period corresponding to the 36th or 38th hour of incubation. B. Later stage, with two pairs of aortic arches.

A. bulbus arteriosus of heart; v. vitelline arteries; 1-5. the aortic arches; the dotted lines indicate the position of the future arches.



system in Vertebrates, the plan is adopted of first describing the development of the circulatory system in Amniota, and afterwards that of the Ichthyopsida. A considerable number of minor points are omitted in order to avoid unduly lengthening the section and complicating the subject.

Very early in the development of the embryo the inner portion of the area opaca (p. 38) becomes so permeated with a network of blood-vessels as to receive the name of the area vasculosa. This net-work soon becomes connected with the embryonic vascular system, but before this is accomplished the heart has already commenced to beat.

The embryonic circulation of Amniotes may be conveniently divided into four sections—(1.) The early stages of the embryonic circulation. (2.) The vitelline circulation. (3.) Later stages of

foetal circulation. (4.) The allantoic circulation. It is impossible to describe the first without considering the others; but it is important to bear in mind the essentially secondary character of the second and fourth systems.

I. Early Stages of Embryonic Circulation.—It is customary to speak of all those vessels which carry blood away from the heart as arteries, and those which return the blood as veins. The arterial system will be described before the venous.

In its earliest stage the arterial system consists of a parallel pair of arteries, each of which arises from the single bulbus

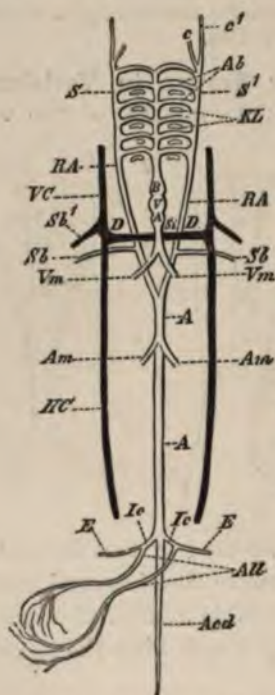


FIG. 165.—DIAGRAM OF THE EMBRYONIC VASCULAR SYSTEM.

[From Wiedersheim.]

A, atrium; A.A. dorsal aorta; Ab. branchial vessels; Acd. caudal artery; All. allantois (hypogastric) arteries; Am. vitelline arteries; B. bulbus arteriosus; c, c'. external and internal carotids; D. ductus Cuvieri (precaval veins); E. external iliac arteries; HC. posterior cardinal vein; Ic. common iliac arteries; KL. gill clefts; RA. right and left roots of the aorta; S, S'. branchial collecting trunks or veins; Sb. subclavian artery; Sb'. subclavian vein; Si. sinus venosus; V. ventricle; Vc. anterior cardinal vein; Vm. vitelline veins.

arteriosus of the heart, and bends round at the anterior end of the pharynx to its dorsal side. Still remaining distinct, each aorta, as it is termed, runs backwards along either side of the notochord below the mesoblastic somites (fig. 176). About half-way down an artery is given off at right angles by each aorta, which, as it passes to the yolk-sac (area vasculosa), is called the vitelline artery (comp. fig. 166, *R.Of.A.*, *L.Of.A.*).

Somewhat later the two aortæ unite together to form a short dorsal aorta, which lies beneath the notochord. The two aortæ soon

separate and dwindle away in the tail. The vitelline arteries arise from each trunk behind the median fusion, and are so large that nearly all the blood passes through them. The arteries which arise from the heart running forwards, upwards, and backwards are known as arches. Thus the dorsal aorta is produced by the junction of a pair of aortic arches. Very shortly afterwards a second and a third pair (figs. 164-167) are developed behind the primitive pair.

The embryonic venous system at this stage consists of an anterior

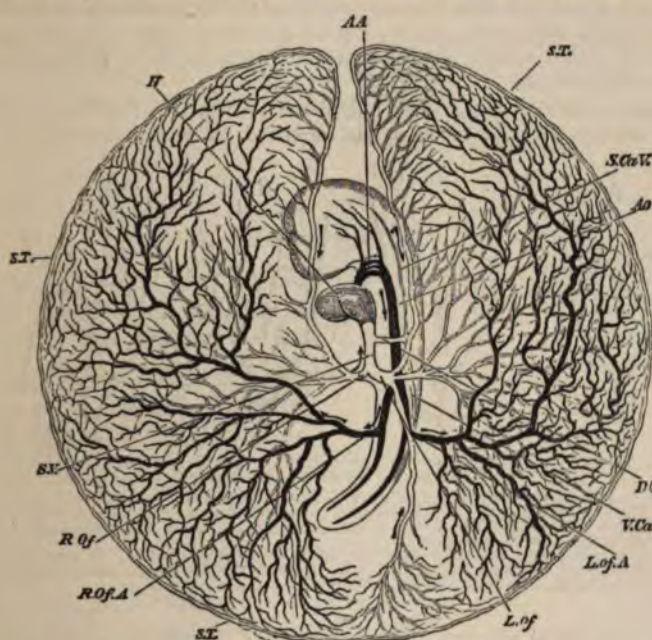


FIG. 166.—DIAGRAM OF THE CIRCULATION OF THE YOLK-SAC OF THE FOWL AT THE END OF THE THIRD DAY OF INCUBATION. [From Foster and Balfour.]

The veins are marked in outline, and the arteries are black. The whole blastoderm has been removed from the egg, and is supposed to be viewed from below, hence the apparent reversal of the sides.

AA, the second, third, and fourth aortic arches; the first has become obliterated in its median portion, but is continued at its proximal end as the external carotid, and at its distal end as the internal carotid; Ao, dorsal aorta; DC, ductus Cuvieri; H, heart; LofA, left vitelline artery; Lof, left vitelline vein; RofA, right vitelline vein; Rof, right vitelline artery; SCaV, superior (anterior) cardinal vein; ST, sinus terminalis; S.F., sinus venosus.

and posterior pair of longitudinal veins (cardinal veins), which run superficial to the aorta. The anterior (superior) cardinal or jugular veins unite with the inferior or posterior cardinals to form a common trunk, ductus Cuvieri (figs. 166, 169), which returns the blood to the heart. Posteriorly the blood is collected from the yolk-sac by the vitelline veins (fig. 166, *Lof*, *Rof*), and transmitted to the heart by the median sinus venosus.

2. Vitelline Circulation.—The vascular supply of the yolk-sac may be conveniently described here. The area vasculosa extends to some distance round the embryo, but it is at first undeveloped in the median line in front of the embryo; it is thus somewhat U-shaped. When the vitelline circulation is first established, the blood enters through the two large vitelline arteries previously mentioned. These arteries divide and subdivide until they terminate in capillary vessels.

The lateral periphery of the area vasculosa is bounded by a blood-vessel, the sinus terminalis, which also extends round the anterior horns of the area and down their inner side. The blood from the capillaries flows in three directions: (1) most of it is collected by the large vitelline veins and conveyed straight to the heart; (2) part flows forward along the anterior portion of the sinus terminalis, round the anterior prolongation, and back along the inner margin of the notch, where it enters the root of the vitelline vein; and (3) lastly, a small quantity proceeds along the posterior half of the sinus terminalis, and is lost in small capillaries, but it ultimately returns by the vitelline veins.

When the vitelline circulation is fully developed (fig. 166), the flow of the blood differs slightly from the condition just described. The sinus terminalis forms a

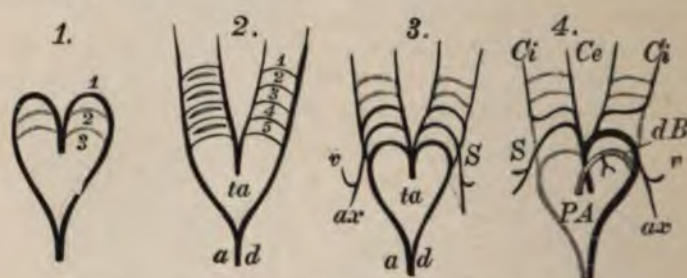


FIG. 167.—DIAGRAMS OF THE AORTIC ARCHES OF A MAMMAL.
[From Landolt and Stirling after Rathke.]

1. Arterial trunk with one pair of arches, and an indication where the second and third pair will develop. 2. Ideal stage of five complete arches; the four clefts are shown on the left side. 3. The two anterior pairs of arches have disappeared. 4. Transition to the final stage.
A, aortic arch; ad, dorsal aorta; ax, subclavian or axillary artery; Ci, external carotid; Ce, internal carotid; dB, ductus arteriosus Botalli; P, pulmonary artery; S, subclavian artery; ta, truncus arteriosus; v, vertebral artery.

complete ring round the area. The distribution of the vitelline arteries and veins is mainly the same, but there is a slight alteration in the second and third channels for the return of the blood. Of the anterior recurrent veins the left is always the larger, and sometimes the right is aborted, so that the blood from the anterior region of the area vasculosa is returned solely by the left anterior recurrent vein. Of course in this case a fusion of the anterior limbs of the area vasculosa has occurred in front of the embryo (fig. 76). On the junction of the lateral halves of the sinus terminalis behind the embryo, the blood is returned by a single median posterior recurrent vein into the left vitelline vein (fig. 166, *Lof*).

3. Later Stages of Fœtal Circulation.—Five pairs of aortic arches make their appearance (figs. 146, 165, 167, 168), but usually the first two have atrophied before the last is formed. The arteries lie towards the inner side of each visceral arch; there is one for the mandibular, hyoid, and each of the three branchial arches.

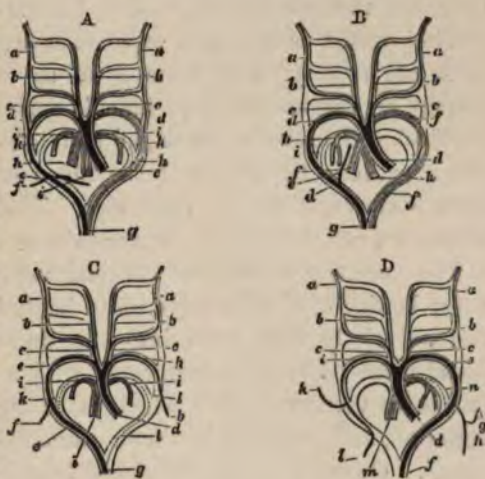
The common ventral trunk (ventral aorta) is continued beyond

the mandibular arch, as the external carotid and the internal carotid is a similar anterior extension of each dorsal aortic trunk (figs. 167, 168, 170). After the disappearance of the first two aortic arches, the aortic trunk connecting the dorsal end of the third arch with the fourth disappears, except in Lizards, but a rudiment, the ductus Botalli, can be traced in some Reptiles. In this manner the internal and external carotids arise from the ventral aorta of the third arch (common carotid), as shown on figs. 167, 168.

The fourth arch always gives rise, as in Amphibia, to the dorsal aorta. This pair of arches persists in Reptiles; but on the longitudinal division of the truncus arteriosus, the channel leading from the left side of the ventricle is continuous with the right

FIG. 168.—DIAGRAM ILLUSTRATING THE TRANSFORMATIONS OF THE AORTIC ARCHES IN A LIZARD, A; A SNAKE, B; A BIRD, C; A MAMMAL, D. Seen from below. [After Rathke.]

a. internal carotid; b. external carotid; c. common carotid. A.—d. ductus Botalli between the third and fourth arches; e. right aortic arch; f. subclavian; g. dorsal aorta; h. left aortic arch; i. pulmonary artery; k. rudiment of the ductus Botalli between the pulmonary artery and the aortic arches. B.—d. right aortic arch; e. vertebral artery; f. left aortic arch; h. pulmonary artery; i. ductus Botalli of the latter. C.—d. origin of aorta; e. fourth arch of the right side (root of dorsal aorta); f. right subclavian; g. dorsal aorta; h. left subclavian (fourth arch of the left side); i. pulmonary artery; k. and l. right and left ductus Botalli of the pulmonary arteries. D.—d. origin of aorta; e. fourth arch of the left side (root of dorsal aorta); f. dorsal aorta; g. left vertebral artery; h. left subclavian; i. right subclavian (fourth arch of the right side); k. right vertebral artery; l. continuation of the right subclavian; m. pulmonary artery; n. ductus Botalli of the latter (usually termed ductus arteriosus).



fourth arch (fig. 168, A, e; B, d), and from it also arise the carotids (c). The left fourth arch (A, h; B, f), is connected with the right side of the ventricle, but it unites with its fellow to form the dorsal aorta (g).

In Birds the right (fourth) aortic arch alone retains its connection with the aorta, the left arch persists as the left subclavian artery (fig. 168, c, h). The reverse occurs in Mammals (fig. 168, D). In both there is a single aortic arch, which springs from the left side of the ventricle.

The fifth arch is known as the pulmonary, as it invariably supplies the lungs; it arises from the right side of the ventricle. In all the Sauropsida the right and left arches persist as the right

and left pulmonary arteries respectively, except in Snakes, in which the left alone persists (fig. 168, B, *h*). In Mammals the left arch disappears, and the right goes to the lungs (fig. 168, D, *m*).

In some forms traces of the communication between the fourth and fifth arches may remain as the ductus Botalli. A comparison of figs. 164-168 will render the development of the adult from the embryonic condition perfectly comprehensible.

The development of the main venous trunks, as it occurs in Birds, will be briefly described as a standard of comparison with other Amniota.

As the embryo increases in size new veins appear, and an anterior (superior) vertebral vein, bringing back blood from the head and neck, and a subclavian from the wing (fig. 169, A, *s.c*) open into the anterior cardinal or jugular vein. The two ductus Cuvieri persist as the superior venæ cavæ. In the lower Mammals there are two superior venæ cavæ, as in Sauropsida, but more usually an anastomosis (left brachio-cephalic or innominate vein) is developed between the right and left jugular veins (fig. 172), and eventually the whole of the blood of the left superior vena cava is conveyed to the right side. The base of the left superior vena cava remains as the coronary sinus.

The posterior or inferior cardinal veins which pass along the outer border of the kidneys unite behind with the caudal veins, and anteriorly they open into the ductus Cuvieri. The intercostal veins begin to be connected with a new longitudinal trunk (posterior vertebral vein), which is continuous with the anterior vertebral, and gradually lose their connection with the posterior cardinals. Owing to their diminished function, the anterior portions of the posterior cardinals disappear; their posterior moieties become the venæ renales advehentes. As a result of this change, the blood from each side of the wall of the body of the embryo, instead of entering the heart through the posterior cardinal, is collected by the posterior vertebral, and, together with the anterior vertebral, passes into the jugular and the ductus Cuvieri (superior vena cava or precaval) (fig. 169, B, *c*).

The two posterior vertebrals are at first symmetrical, but in Reptiles, when transverse anastomoses develop between them, the right becomes the larger. In Mammals (fig. 171) the left posterior vertebral usually becomes rudimentary, and is known as the hemiazygos vein; it is connected by a transverse anastomosis with the right posterior vertebral or azygos vein.

While these changes have been going on, a new and important vein, the vena cava inferior, has made its appearance. At first it is a small vein arising in two roots from the inner border of the kidneys, and unites with the allantoic vein (to be described shortly) before it enters the heart. The atrophy of the anterior portion of the posterior cardinals is doubtless due to the newly developed vena cava inferior carrying the venous blood of the kidney direct to the heart. On its way to the heart the vena cava inferior passes through the liver, from which it receives a few vessels, *venæ reheventes* (fig. 169, B).

Renal Portal System.—In Reptiles the blood from the caudal veins and the posterior portion of the posterior cardinal veins (*venæ renales adheventes*) is broken up into capillaries in the

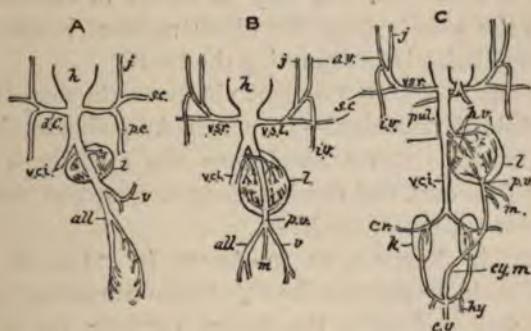


FIG. 169.—DIAGRAM OF THREE STAGES IN THE DEVELOPMENT OF THE VENOUS CIRCULATION OF THE FOWL. [After Balfour.]

A. At the commencement of the fifth day. B. During the later days of incubation. C. At the commencement of respiration by means of the lungs.
all. allantoic (anterior abdominal) vein; *a.v.* anterior (superior) vertebral vein; *cr.* crural veins; *c.v.* caudal vein; *cy.m.* coccygeo-mesenteric vein; *d.C.* ductus Cuvieri; *d.v.* ductus venosus; *h.* heart; *hy.* hypogastric veins; *h.v.* hepatic vein; *i.v.* inferior vertebral vein; *j.* jugular vein (superior or anterior cardinal); *k.* kidney; *l.* liver; *m.* mesenteric vein; *p.c.* posterior (inferior) cardinal vein; *pul.* pulmonary vein; *p.v.* portal vein; *s.c.* subclavian vein; *v.* vitelline vein; *v.c.i.* vena cava inferior; *v.s.f.* right superior vena cava. The ductus venosus passes through the liver in A and B.

kidneys, and passes thence to the heart by the vena cava inferior. This is known as the renal portal system.

In Birds and Mammals this does not occur; the blood from the tail and hind-limbs passes directly into the vena cava inferior, and not indirectly through the kidneys. This comes about in Mammals by the development of the common iliac veins, which collect the blood from the hind-quarters; the posterior portion of the cardinal veins enter the common iliac as the hypogastric (fig. 169, C, *hy*).

Hepatic Portal System.—As has already been described, the blood from the yolk-sac is conveyed by the vitelline veins direct to the heart. A small vein early appears in connection with

developing mesenteron. This mesenteric vein (fig. 169, B and C, *m*) joins the vitelline vein; their common trunk (ductus venosus or omphalo-mesenteric trunk) becomes enveloped within the rapidly growing liver, and sends off branches into that viscus. As these branches increase in size they convey more and more blood, and the ductus venosus, which originally passed directly into the heart, is proportionately diminished, until eventually all the blood from the yolk-sac and mesentery passes into the hepatic branches, *venæ adheventes*, and is collected by the *venæ reheventes* and transmitted to the vena cava inferior. There is nothing remarkable in the association of the vitelline and mesenteric veins, as it has been already shown that the yolk-sac is practically merely the hypertrophied ventral wall of the mesenteron, consequent upon the occurrence of food-yolk. It may be stated in another way by saying that the vessels from the digestive tract break up in the liver into capillaries before entering the heart.

In Birds and Mammals the right vitelline vein soon disappears.

4. **Allantoic Circulation.**—There is in Amphibia a vein, anterior abdominal, which receives blood from the hind-limbs and from the urocyt (bladder), and passing along the median ventral wall of the abdomen it enters the liver.

There are in Reptiles, as in Anura (p. 234), at first two anterior abdominal veins developed. These run along the anterior abdominal wall and enter the ductus Cuvieri; posteriorly they are connected with the system of the posterior cardinal by the epigastric veins, and also with the bladder. On account of the precocious development of the bladder to form the allantois, these veins are known as allantoic veins. The left disappears, so that a single allantoic vein enters the heart after having been joined by the inferior vena cava. Later the two unite nearer the liver, and finally the anterior abdominal (allantoic) vein joins the portal system.

In Birds the two anterior abdominal veins unite and fall into the ductus venosus (fig. 169, B); the single stem comes to be very long, owing to the rapid growth of the allantois, and it forms the allantoic vein. The right anterior abdominal disappears; the left bifurcates on reaching the allantois (fig. 169, B, *all*).

The vitelline veins are at first very large (fig. 166), and the allantoic vein quite small, but their relative size is reversed as the allantois increases and the yolk-sac diminishes in importance. The mesenteric vein joins these two, and thus the large portal

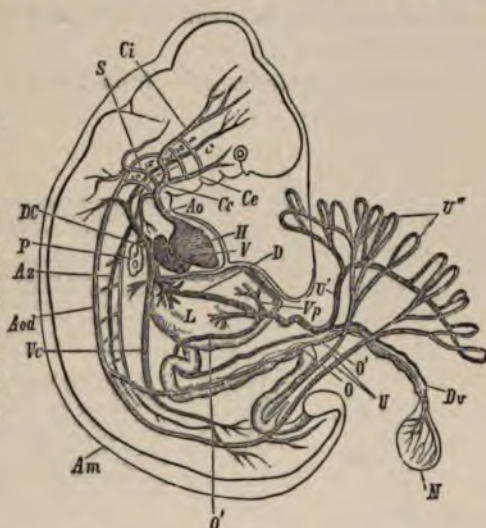
vein is formed. Although the allantoic vein disappears before hatching, the caudal and posterior pelvic veins are connected with the portal vein in the adult by the coccygeo-mesenteric vein (fig. 169, *C, cy, m*).

In Mammals the two primitive anterior abdominal (allantoic) veins are very early developed, and unite in front with the vitelline vein. The right allantoic vein (fig. 171, *B, u'*), like the right vitelline vein (*o'*), soon disappears. The long common trunk of

FIG. 170.—DIAGRAM OF THE ARRANGEMENT OF THE PRINCIPAL VESSELS IN A HUMAN FETUS.

[From Claus after Ecker.]

Ao. aortic trunk; *Am.* amnion; *Aed.* dorsal aorta; *Az.* azygos vein; *C.* anterior cardinal vein; *Ce.* common carotid; *Ce.* external carotid; *Cl.* internal carotid; *D.* ductus venosus Arantii; *DC.* ductus Cuvieri; *Dr.* vitelline duct; *H.* ventricle; *L.* liver; *N.* umbilical vesicle (yolk-sac); *O.* vitelline (omphalo-mesenteric) artery; *O'.* vitelline vein; *P.* lung; *S.* subclavian artery; *U.* allantoic (umbilical) arteries with their placental ramifications; *U'*, *U'* allantoic vein; *V.* auricle; *Vc.* vena cava inferior; *Vp.* portal vein; 1, 2, 3, 4, 5, the arterial arches—the persistent left aortic arch is not visible.



the (left) allantoic and vitelline veins (ductus venosus) passes through the liver.

In its passage through the liver, according to Kölliker, the ductus venosus gives off branches near its entrance, and receives branches from the anterior end of the liver (fig. 171, *B*). The main duct, unlike what occurs in the Sauropsida, persists throughout life as the ductus venosus Arantii (fig. 171, *D, l*).

When the placenta is developed, the allantoic circulation becomes extremely important. The vitelline vein, on the other hand, is greatly reduced, and, with the larger mesenteric vein, it constitutes the portal vein. Later the portal vein (fig. 171, *D, p*) enters one of the venæ advehentes of the allantoic vein (*p'*).

The vena cava inferior and the ductus venosus at first unite together and enter the heart by a common trunk (fig. 171, *A, ci, l*) Owing to the increased size of the former, the venæ reheventes or hepatic veins open into it, and not into the ductus venosus. The

ductus venosus itself (ductus venosus Arantii) comes to be a small branch of the vena cava (fig. 171, D).

The allantoic vein degenerates at the end of foetal life into the solid cord known as the round ligament, and all the venous supply of the liver comes from the portal vein.

Beddard finds that there is in the adult *Echidna* an anterior abdominal (allantoic) vein, which arises from the under surface of the bladder, and passing along the ventral wall of the body, is distributed to the left half of the liver.

An anastomosis between the iliac and portal veins is not established in Mammals.

The allantoic arteries arise from the dorsal aorta as branches of

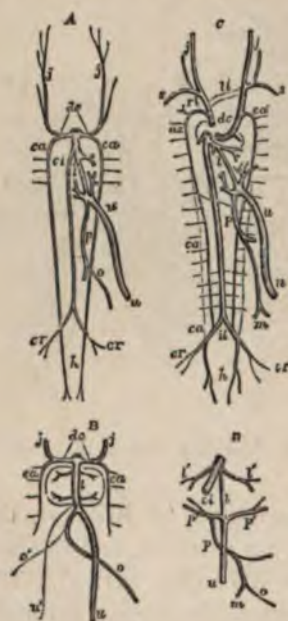


FIG. 171.—DIAGRAMS ILLUSTRATING THE DEVELOPMENT OF THE GREAT VEINS IN MAMMALS. [From Quain after Kölliker.]

A. Plan of the principal veins of the human embryo of about four weeks, or soon after the first formation of the vessels of the liver and the vena cava inferior. B. Hepatic circulation at a somewhat earlier stage. C. Principal veins of the foetus at the time of the first establishment of the placental circulation. D. Hepatic circulation at the same period.

az, azygos vein, above p (in C)—the oblique line is the vein by which the hemiazygos joins the azygos vein; ca, posterior cardinal veins; ca' (in C) the remains of the left cardinal vein by which the superior intercostal veins fall into the left innominate vein; cr, external iliac or crural veins; ci, vena cava inferior; dv, ductus Cuvieri; A, hypogastric or internal iliac veins, in the line of continuation of the primitive cardinal veins; dl, the division of the vena cava inferior into the common iliac veins; j, jugular or anterior cardinal veins; l, ductus venosus; l', hepatic veins; h, (in C) in dotted lines, the transverse branch of communication between the jugular vein which forms the left innominate vein; m, mesenteric veins; o, vitelline or omphalo-mesenteric vein; o', right vitelline vein; p, portal vein; p/p', venae advehentes; ri, right innominate vein; s, sub-clavian vein; u, allantoic, umbilical or (left) anterior abdominal vein; w, (in B) the temporary right allantoic vein.

the common iliac arteries (figs. 165, *Ic*, 171, *U*). On the disappearance of the allantois they remain as the hypogastric arteries.

Circulation in Ichthyopsida.—Having now described the development of the circulation in the Amniota, it will be necessary to briefly refer to the circulation in Ichthyopsida.

Fig. 165, which represents the embryonic circulation of an Amniote in a diagrammatic manner, will, with a few alterations, serve to illustrate the circulation in Fishes. The vitelline arteries (*Am*) and the allantoic arteries (*All*) are not present, and the

blood from behind is returned to the heart by the subintestinal vein, and not by the vitelline veins (*Vm*).

The first or mandibular arterial arch is represented by a small vessel which arises from the branchial vein of the hyoid arch, and supplies the rudimentary gill (pseudobranch) of the spiracle. In other Fish this artery of the first arch disappears.

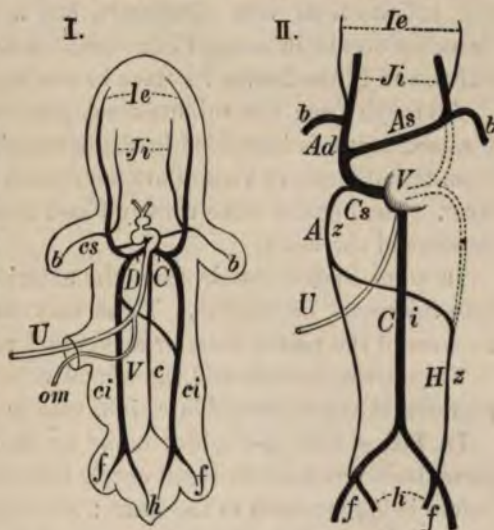
The second or hyoid arterial arch is functional throughout life in Elasmobranchs; usually it remains as a small vessel which goes to the pseudobranch of the hyoid. The artery is said to persist in Protopterus amongst the Dipnoi.

The air-bladder is supplied with arterial blood from the celiac artery or direct from the aorta, except in some Ganoids (Polypterus

FIG. 172.—VENOUS CIRCULATION IN MAMMALIAN EMBRYO. [From Landois and Stirling.]

I. Early arrangement of veins.
II. Final disposition.

Ad. right innominate vein; *As.* left innominate vein; *Az.* azygos vein; *b.* subclavian veins; *ci.* vena cava inferior; *ci.* posterior vertebral veins; *Cs.* vena cava superior; *cs.* anterior cardinal vein; *DC.* ductus Cuvieri (superior vena cava); *f.* external iliac vein; *h.* hypogastric vein; *Hs.* hemiazygos vein; *Ie.* external jugular vein; *Ji.* internal jugular vein; *om.* vitelline or omphalo-mesenteric vein; *U.* umbilical or allantoic vein; *V.* ventricle; *Vc.* vena cava inferior.



and *Amia*) and Dipnoids, where the last branchial arch sends an artery direct to the air-bladder.

In *Amphibia* the first aortic arch (mandibular) is never developed, and the second (hyoid) arises later than the succeeding arches; it never unites dorsally with the latter, and only gives rise in part to the lingual artery.

Of the four branchial aortic arches present in larval *Amphibia*, only the second, in the *Anura*, retains its connection with the dorsal aorta. The first becomes the carotid arch, and gives rise to the carotids; the second forms the systemic arch; the third is rudimentary or absent (*Anura*) in the adult, while the fourth or pulmonary supplies the lungs. A narrow anastomosis or ductus

Botalli may unite the second, third, and fourth arches in adult Urodeles.

The venous system of Fishes primitively consists of a median unpaired subintestinal vessel extending from the end of the tail to the heart; indeed, the heart may be considered as a specialised portion of this vessel. Later, cardinal veins are developed, as in Embryonic Amniotes, but in Fishes they persist as the main venous trunks. The caudal portion of the subintestinal vessel acquires a secondary connection with the posterior cardinal veins. In some cases this, its anastomosis, breaks up into capillaries in the mesonephros, thus forming a renal portal system.

After the appearance of the cardinal veins the main portion of the subintestinal vein disappears, but a remnant of one of its branches occurs in some Elasmobranchs as the vein of the spiral valve, and it also leaves its trace in the hepatic portal system.

A branch from the subintestinal goes to the yolk-sac, and the common trunk is imbedded in the developing liver. Later, vessels from the alimentary viscera are developed, which break up in the liver. The hepatic veins convey blood from the liver to the sinus venosus of the heart.

In some Fishes vessels from the anterior abdominal wall enter into the portal circulation. These may be regarded as the fore-runners of the paired anterior abdominal veins.

The ductus venosus and the caudal vein may be regarded as the representatives of the subintestinal vein in Amniota.

In Fishes the air-bladder ranks as an ordinary viscus of the mesenteric series, as its blood enters into the hepatic portal system before being returned to the heart; the only exception occurring is in the Dipnoi, where the pulmonary vein, as it may now be called, carries the blood direct to the left auricle. The same obtains in Amphibia.

The Amphibia initiate a new departure in the development of a vena cava inferior, which functionally replaces the larval posterior cardinal veins. The hepatic veins enter into the vena cava inferior. On the disappearance of the posterior cardinals the ductus Cuvieri (superior venæ cavæ) are connected only with the anterior cardinals (jugular veins).

At first two anterior abdominal veins occur, and open anteriorly into the sinus venosus, having previously united with a vein from the truncus arteriosus. An epigastric branch from the iliac vein and veins from the urocyst or bladder (allantois) join them, after

which they unite into a single vessel. The atrophy of the right vein is said to result in a single anterior abdominal vein. A secondary connection occurs between the anterior abdominal and the portal system, which persists in the adult.

In other respects the Amphibia are essentially piscine in their vascular system.

Summary of the History of the Aortic Arches.—As there is still some uncertainty concerning the fate of some of the aortic arches in the various groups of Vertebrates, it may not be superfluous to briefly recapitulate the facts as at present known. In this summary, as in the foregoing account, the view is adopted which is most generally current, viz., that there is one prehyoid aortic arch, usually termed the mandibular or first aortic arch, the hyoid is the second, while in most Fishes there are four branchial aortic arches. Dohrn terms the aortic arch immediately in front of the hyoid the *arteria thyreoidea mandibularis*, or shortly the thyroid artery (the mandibular of Balfour), which, in Elasmobranchs, after receiving a venous commissure from the hyoid arch, is called the spiracular artery, as it supplies the spiracle.

First aortic arch (mandibular?), present in all embryonic Vertebrata, except the Amphibia, only persisting in Elasmobranchii, and that imperfectly, as the spiracular artery.

Second aortic arch (hyoid), present in all embryonic Vertebrata, but imperfect in larval Amphibia. Persistent in Elasmobranchii, usually so in Ganoidei, rudimentary in Teleostei (as artery of pseudobranch), may disappear in some Dipnoi, and partially persists as the lingual artery in Amphibia and Amniota.

Third aortic arch (first branchial), present in all larval forms, and persists as a complete arch in all Fishes. In adult Amphibia and Amniota it loses its connection with the other arches and gives rise to the common carotid trunks.

Fourth aortic arch (second branchial), retains its connection with the dorsal aorta throughout the Vertebrate series.

Fifth aortic arch (third branchial), persists in all adult Fishes, and to a diminished degree in adult Urodela (still uniting with the dorsal aorta), is lost during the metamorphosis of Anura [Boas], and disappears in the Amniota.

Sixth aortic arch (fourth branchial), persists throughout the Vertebrate series. In some Ganoidei (*Polypterus*, *Amia*) and Dipnoi also giving a branch to the air-bladder, and in adult Amphibia and Amniota supplying the lungs. In adult Urodela alone is a connection still left with the dorsal aorta, and in Anura a large cutaneous branch is given off.

It is usually stated that the pulmonary artery of Anura and Amniota is the third branchial aortic arch, and that the fourth disappears. The subject requires reinvestigation, as probably there is a fusion of these two arches, both of them losing their connection with the dorsal aorta, but the fourth branchial still giving origin to the pulmonary artery. Boas has shown that this is actually the case in the young Frog, and in *Salamandra* the third branchial arch has the appearance of a diminishing artery. It is, moreover, very improbable that the arterial supply of the lungs should shift from the last arch to the one in front of it. If this be admitted, the term "fifth aortic arch" in the above description of the development of the arterial arches in Amniota must be understood as implying fifth+sixth aortic arch, making seven arches in all.

Changes Undergone in the Circulation of Fœtal Mammals.—The earliest phases in the circulation have already been described. Later all the venous blood passes directly into the right auricle. The venous blood from the head and upper portion of the body is returned by the two *venæ cavæ superiores* (innominate veins). In most Mammals the proximal portion of the left superior vena cava atrophies; so all

the blood from the right and left sides of the anterior region of the body comes to be returned by the single (right) superior vena cava.

The primitive posterior cardinal veins, and later the posterior vertebrals (azygos and hemiazygos), convey blood from the latero-dorsal walls of the trunk to the superior vena cava. The venous blood of the cardiac circulation passes by the coronary vein into the right auricle.

The main portion of the blood from the hinder region of the body is brought back by the vena cava inferior, which is by this time rapidly rising into importance. The decreasing blood from the yolk-sac and the gradually increasing mesenteric venous blood passes by the portal vein into the allantoic vein (here known as the ductus venosus), which passes straight through the liver and enters the right auricle along with the vena cava inferior. At its entrance into the liver the ductus venosus gives rise to a few veins (*venæ advehentes*), and receives again a small number of veins (*venæ reheventes*) before leaving that viscus. The liver is also supplied with arterial blood by a branch (hepatic artery) from the dorsal aorta. As the vena cava inferior increases in size the hepatic veins (*venæ reheventes*) open into it.

The blood of the superior vena cava passes ventral and to the right side of the Eustachian valve, and, together with a small quantity of blood from the inferior vena cava, passes into the right ventricle, and thence along the pulmonary artery to the lungs. During fetal life the latter are not distended; consequently only a very small quantity of blood is concerned in the pulmonary circulation: this is returned by the pulmonary veins to the left auricle. The remaining blood passes through the wide ductus arteriosus (Botalli) (figs. 167, 168) into the dorsal aorta, just beyond the spot where the carotid and subclavian arteries arise.

Only a small portion of the blood returned by the vena cava inferior passes into the right ventricle; by far the greater portion is diverted by the Eustachian valve through the foramen ovale into the left auricle, and thence, together with the small quantity of blood returned from the lungs by the pulmonary veins, passes into the left ventricle, then it passes along the ascending arch of the aorta (fourth aortic arch of the left side), and is mainly distributed to the head and fore-part of the body by the carotid and subclavian arteries. A small quantity probably passes along with the blood from the ductus arteriosus down the descending or dorsal aorta.

To recapitulate, and omitting minor details:—The blood from the anterior region of the body enters the right auricle by the superior vena cava, thence to the right ventricle and pulmonary artery. A small quantity passes to the lungs and back to the right auricle (pulmonary circulation); the greater portion flows through the ductus arteriosus to the dorsal aorta, and thence to the posterior region of the body. This blood is returned by the vena cava inferior to the right auricle, where it is diverted by the Eustachian valve to the left auricle, and, entering the left ventricle, passes by the aortic arch to the anterior region of the body.

It will be evident from the above that the blood returned by the allantoic veins is distributed to the anterior region of the body after passing through the liver. Thus the large developing brain is supplied with the most nutritious and aerated blood available, while the grosser organs have distributed to them the blood which has already circulated through the anterior region of the body. A large portion of the blood from the dorsal aorta passes into the allantoic (placental) circulation, and becomes partially purified in the placental villi by diffusion of gases with the maternal blood. In the embryo, as in the adult, it is the right ventricle which pumps the blood into the respiratory organ (*i.e.*, placenta or lungs).

During the later portion of intra-uterine existence, the blood returned by the inferior vena cava increasingly mixes with that of the superior vena cava, and a gradual approach to the adult arrangement is observable.

The rapid dilatation of the lungs and the loss of the placenta at birth result in a considerable modification in the circulation.

The vessels of the distended lungs become filled with a large quantity of blood, which, being returned into the left auricle, equalises the pressure of the blood on each side of the auricular septum, and no blood passes from one auricle into the other. The free fold of the foramen ovale gradually becomes fused with the margin of the foramen, and thus permanently completes the septum. As was previously mentioned, this valvular fold of the auricular septum was so arranged that, even during foetal life, blood could only flow from the right into the left auricle. A larger or smaller portion of the foramen ovale may remain unclosed for a long period, or even throughout life.

The ductus arteriosus rapidly diminishes in size, and normally entirely disappears; the same fate also befalls the allantoic (umbilical) arteries. The allantoic (umbilical) vein is obliterated as far as its entrance into the liver, and the ductus venosus disappears within that organ.

Excretory Organs.—An excretory organ consists essentially of a tube or duct which leads from the interior of the animal to the exterior; such a tube is termed a nephridium.

The internal orifice of a nephridium opens into the archicœl (Platyhelminths) or coelom (Cœlomata); in the latter case the special part of the coelom into which it enters may be more or less separated from the general body-cavity; thus the nephridium may open into the pericardium or into a Malpighian body (Vertebrates). The orifice itself (nephrostome) may be funnel-shaped and richly ciliated, the cilia working outwards; or there may be a single long cilium, which has a screw-like action, lying within the nephrostome (Platyhelminths, Rotifers).

The tube itself may be straight, bent upon itself, or coiled. Each tube may either open independently to the exterior (Invertebrates), or the nephridia of each side may communicate with a common duct which opens posteriorly (Vertebrates).

A pair of nephridia only may be present (Platyhelminths, Rotifers, Nematodes, Gephyrea, Polyzoa, Brachiopoda, Mollusca), or numerous pairs may occur, in which case there may be a single pair (most Chætopoda, a few Vertebrata) or several pairs of nephridia for each segment of the body in which they occur.

In addition to carrying away nitrogenous waste, the nephridia, or some of them, may also act as the efferent ducts of the generative organs (Brachiopods and some Chætopods, Molluscs, and vasa efferentia of Vertebrates).

Invertebrates.—Our knowledge of the development of the excretory organs of Invertebrates is in a very unsatisfactory condition.

The excretory system of Platyhelminths and Rotifers consists in the main of a pair of lateral longitudinal vessels, from which

numerous fine branches arise which open into the interstices of the spongy mesenchyme (archicœl), into the blood-vessels in some Nemerteans (according to Oudemans), or into the "body-cavity" of Rotifers. The longitudinal trunks may open anteriorly or posteriorly either independently or by a common orifice; in the latter case the conjoint vessels may expand into a contractile vesicle. In Nemerteans the nephridial canals communicate with the exterior by one or numerous ducts, which are always situated above the nerve-trunks [Oudemans].

The only observations on the development of this system are those of Hubrecht's for the Nemertean Worm (*Lineus obscurus*). He finds that a pair of vesicular outgrowths arise from the hypoblastic œsophagus; although their further development could not be traced, he believes they are the rudiments of the nephridia.

The paired segmental organs or nephridia of Chætopods appear to be developed from the peritoneal epithelium of the body-cavity, either on the posterior wall of the transverse septa or on the body-wall. The external opening is secondarily acquired.

There are several forms of excretory organs amongst Arthropods. *Peripatus* possesses segmental organs similar to those of Annelids, except that, from Balfour's account, they appear to be devoid of cilia. The Amphipod Crustacea have hypoblastic intestinal cæca (pp. 169, 186), while the Insects have epiblastic rectal Malpighian tubules (p. 111). The excretory organs of the Decapod Crustacea are the green glands situated in the basal joint of the antennæ, the outer chamber of which appears to be developed as an epiblastic invagination. The so-called shell-glands of Crustacea may also be excretory organs.

Provisional renal organs are developed in the embryos of most of the groups of Odontophorous Mollusca. A pair of V-shaped tubes, with an internal opening into the cavity of the head and an external orifice on the ventral surface behind the mouth, is present in the aquatic Pulmonata, and possibly in some other forms. Rabl and Hatschek ascribe to them a mesoblastic origin, but Fol states that they arise as epiblastic invaginations. Certain epiblastic larval excretory organs have already been described (p. 108).

The adult renal organ (organ of Bojanus) has been variously described to have an epiblastic and a mesoblastic origin. Rabl states that in *Planorbis* a mass of mesoblast cells appears near the end of the intestine, which, becoming vesicular, attaches itself to

the epiblast to the left of the anus, and acquires an external opening. The internal pericardial orifice does not appear to be acquired till after the formation of the heart.

Chordata.—No distinct urinary organs occur in Ascidians, unless the neural gland has this function.

Hatschek has recently discovered a true kidney in *Amphioxus*, which has the structure and development of a nephridium. It develops in the larva as a mesodermal ciliated funnel and canal on the left side only of the mouth in the region of the first somite. In the adult the nephridium lies in a narrow portion of the body-cavity, near the ventral body of the notochord, overlying the left carotid (which is a continuation of the left aorta). It appears to open into the pharynx.

The Vertebrate excretory system consists of three parts—(1.) Head-kidney or Pronephros; (2.) Wolffian body or Mesonephros; (3.) Kidney proper or Metanephros. These three portions are never functional at the same time, and are to be regarded as differentiations of the primitive kidney which have occurred in the evolution of the Vertebrates.

1. Pronephros.—The first part of the excretory system to develop is the duct—variously termed segmental duct, pronephric duct, the duct of the primitive kidney, or archinephric duct. The pronephros, when present, is always connected with the anterior extremity of this duct.

The following is the generally received account of the development of the segmental duct, but the duct has been shown by several investigators to have an *epiblastic* origin (fig. 178*, *s.d.*). The significance of this will be shortly pointed out (p. 249).

In the Amphibia the segmental duct appears as a groove (fig. 173, A, *s.d.*) along the outer angle of the dorsal region of the body-cavity, which commences just behind the branchial region. The groove is continuously constricted off from before backwards so as to form a canal or duct; except anteriorly, where the constriction only takes place at intervals, leaving two (*Urodela*), three (*Anura*), or four (*Cæcilia*) openings. The short tubes connecting these openings or nephrostomata with the segmental duct increase in length and form the segmental tubes, which correspond in number with the segments which the pronephros occupies.

The duct immediately behind these tubules becomes coiled. A vascular process from the peritoneum, the glomerulus, projects on each side of the aorta into a dilated section of the body-cavity,

which becomes partially cut off from the rest of the coelom (fig. 173, B). The whole of these structures collectively constitutes the pronephros.

The segmental duct eventually opens posteriorly into the cloaca.

The pronephros develops in the Teleostei in a similar manner, except that there is only one anterior opening (nephrostome); and the part of the body-cavity into which it opens, and in which the glomerulus lies, becomes completely constricted off, so as to form what is practically an enormous Malpighian body (fig. 173, C).



FIG. 173.—PRONEPHROS OF ICHTHYOPSIDA.

A. Transverse section through a very young Tadpole of a Toad (*Bombinator*) at the middle of the body. [After Götte.] B. Diagram illustrating the partial isolation of the glomerulus within a pouch of the body-cavity. C. Transverse section through the pronephros of a Trout ten days before hatching. [After Balfour.] D. Diagram of the pronephros of *Lepidosteus*. [After Balfour and Parker.]

ao, dorsal aorta; b.c. body-cavity; ep. two-layered epiblast; f. peritoneal funnel; gl. glomerulus; m. mesenteron; m.p. muscle-plate; n. neural tube; nch. notochord; n.s. nephrostome; p.o. opening of pronephric tubule into the isolated portion of the body-cavity; s.d. segmental duct; som. somatic, and sp.m. splanchnic, mesoblast; t. pronephric tubule; x. subnotochordal rod; y.hy. yolk hypoblast.

The same arrangement occurs in young larvæ of the Ganoid *Lepidosteus* (Balfour and Parker), except that a tubular communication with the body-cavity (fig. 173, D) is retained for some time.

It is usually stated that in some Teleosts the head-kidney (pronephros) is the only excretory organ of the adult; in most it occurs together with the Wolffian body (mesonephros), and in a few it disappears altogether. Balfour, however, has shown that in certain typical forms (and therefore probably in all) the pronephros, when it persists, loses its excretory function and degenerates into a lymphatic gland. In those specialised Teleosts (*e.g.*, *Lophius*) in which the pronephros only is supposed to occur, the mesonephros has probably been mistaken for that organ. Weldon suggests that the head-kidney of Teleosts may be regarded as a suprarenal body.

The pronephros occurs in all the Ichthyopsida, except the Elasmobranchii, but only functions during a period intervening between hatching and the attainment of full maturity; in other words, the pronephros is always a larval organ, and never con-

stitutes an active part of the excretory system in the adult state. It is either absent or imperfectly developed in those types (Elasmobranchii and Amniota), which undergo the greater part of their development within the egg or before birth.

In the Elasmobranchs the segmental duct arises anteriorly as a solid ridge of cells from the somatic layer of the intermediate cell-mass. From this ridge a solid column of cells grows back to the cloaca without coming into contact with any neighbouring structures. A central cavity or lumen soon appears, and the duct opens widely into the body-cavity anteriorly.

The development of the pronephros has been most carefully studied in the Fowl. In this form the segmental duct arises as a solid ridge from the parietal mesoderm, just ventral to the muscle-plates. The ridge, which extends to five segments, is constricted

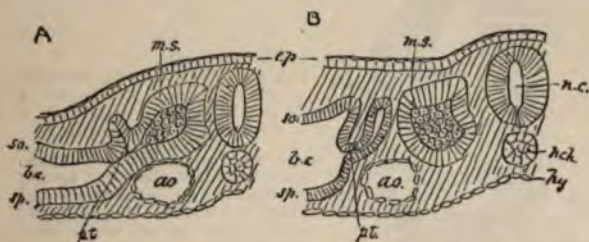


FIG. 174.—DIAGRAMS ILLUSTRATING THE DEVELOPMENT OF THE PRONEPHROS IN THE FOWL.

ao. aorta; b.c. body-cavity; ep. epiblast with its epitrichial layer; hy. hypoblast; m.s. mesoblastic somite; n.c. neural canal; nch. notochord; p.t. pronephric tubule; so. somatic, and sp. splanchnic, mesoblast.

off at intervals from the intermediate cell-mass, but remains attached at certain points. The duct grows backwards as in Elasmobranchs. The further history of this duct will be described later. The pronephros extends in the Fowl over the seventh to the eleventh segments inclusive, the most anterior mesoblastic somite behind the auditory involution being counted as the first.

As the pronephros is the first part of the excretory system to be developed, and often is the sole excretory organ for a considerable period, it is usually concluded that it and its duct (the segmental duct) are the most primitive parts of the vertebrate excretory system. The mode of its development in the Amphibia may also be regarded as primitive, especially since Shipley has shown that the anterior portion of the pronephros of the Lamprey develops in a similar manner.

2. **Mesonephros.**—The Wolffian body or mesonephros is largely

developed in all Vertebrates, but it does not persist as an excretory organ in adult Amniota.

The mesonephros consists of a number of serially arranged primary tubules, segmental or Wolffian tubules, which may be segmentally arranged (Elasmobranchs, some Amphibia, and at first in Reptiles), but usually a variable number of tubules are formed in each segment. Each tubule opens on the one hand into the segmental duct, and on the other into a Malpighian body. The latter sometimes (Elasmobranchs and Amphibia) communicates with the body-cavity by a short tube (peritoneal funnel). In addition to the primary tubules there may be an inconstant number of dorsally placed secondary, tertiary, &c., tubules, which correspond with and are developed from the primary tubules.

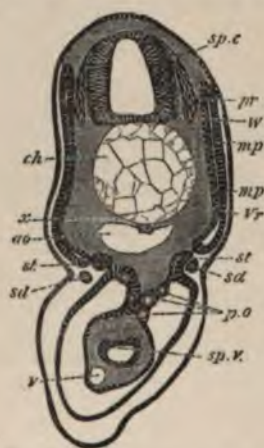


FIG. 175.—TRANSVERSE SECTION THROUGH THE TRUNK OF A YOUNG EMBRYO ELASMOBRANCH (*Seyllium*). [From *Balfour*.]

ao, dorsal aorta; ch, notochord; mp, somatic, and mp', splanchnic, layer of muscle-plate; p.c, primitive germinal cells; pr, dorsal root of spinal nerve; sd, segmental duct; sp.v, spiral valve of intestine; vr, rudiment of vertebral body; W, white matter of spinal cord; x, subnotochordal rod.

These dorsal secondary tubules resemble in their structure the primary tubules, and usually open into the latter just before they enter the segmental duct. In the larval Amphibia only, the secondary and other tubules are known to have peritoneal funnels arising from their Malpighian bodies. It is worthy of note that the nephrostomata are connected with the Wolffian tubules in larval Anura, but that later on they become separated from them, and open into the renal-portal vein [Wiedersheim].

The primary Wolffian tubules are usually stated to be derived as solid ingrowths from the peritoneum towards the segmental duct; but Sedgwick has shown that in Elasmobranchs they have the following development. It has previously been stated (p. 212) that the muscle-plates of Elasmobranchs are dorsal extensions of

the body-cavity, which become cut off (fig. 150, *m.p.*) by the coming together of the somatic and splanchnic mesoblast. The continuous non-segmented band of cells connecting the non-segmented muscle-plates with the peritoneal epithelium being known as the intermediate cell-mass. Sedgwick found that the passage connecting the body-cavity with that of the muscle-plates persists for some time. Its connection with the ventral dilation of the muscle-plate cavity is carried ventralwards as far as the outer dorsal corner of the segmental duct, so that it appears as a canal opening into the body-cavity just internal to the segmental duct, and thence curling

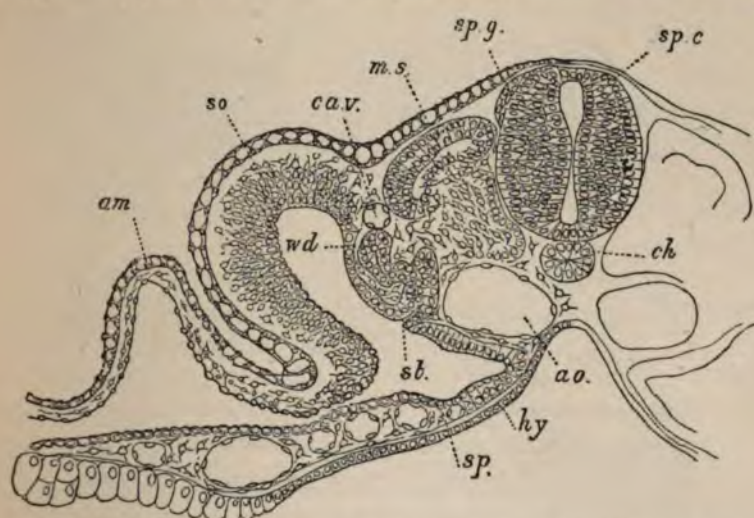


FIG. 176.—TRANSVERSE SECTION THROUGH THE TRUNK OF A DUCK EMBRYO WITH ABOUT TWENTY-FOUR MESOBLASTIC SOMITES. [From Balfour.]

am., amnion; *ao.*, aorta; *ca.v.*, cardinal vein; *ch.*, notochord; *hy.*, hypoblast; *m.s.*, muscle-plate; *so.*, somatopleur; *sp.*, splanchnopleur; *sp.c.*, spinal cord; *sp.g.*, spinal ganglion; *st.*, segmental tube; *wd.*, Wolffian (segmental) duct.

round its dorsal wall, opens into the muscle-plate cavity. The ventral wall of this passage is formed of large columnar cells, the inner and dorsal wall of much flatter cells.

At the next stage of development the passage becomes quite separated from the muscle-plate cavity, and now lies as a blind tube (fig. 175, *st*) opening into the body-cavity internal to the segmental duct, with which it soon unites and forms a segmental tubule.

Sedgwick has also further shown that in the Fowl, in the region of the body between the twelfth and fifteenth somites inclusive, the segmental tubes (Wolffian tubules) have a double origin: (1)

from outgrowths from the Wolffian or segmental duct; (2) as parts of the intermediate cell-mass.

The intermediate cell-mass is at first continuous with the peritoneal epithelium in every section, but this connection soon becomes lost at certain points and maintained at others. At the points where the continuity is retained, a peritoneal funnel is subsequently formed by the development of a lumen extending from the body-cavity into the intermediate cell-mass.

The tubules have at this stage their characteristic and well-known S-shape (fig. 176). They consist of the following parts:—

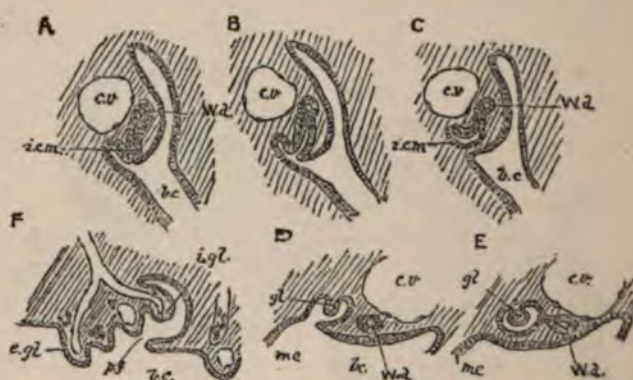


FIG. 177.—EARLY STAGES IN THE DEVELOPMENT OF THE WOLFFIAN BODY IN THE FOWL. [After Sedgwick.]

A—C. A series of successive sections through the thirteenth segment of an embryo with thirty-one or thirty-two segments, A being the most anterior. In A and B the tubule is connected with the peritoneal epithelium; and a lumen has appeared in it, which is continued behind into the part of the tubule separated from the peritoneal epithelium, as in C.

D—E. Sections through the thirteenth or fourteenth segment of an embryo with thirty-four or more segments, showing the first appearance of the external and internal glomeruli. D and E correspond to, and are further developments of, B and C.

F. Diagrammatic longitudinal vertical section, showing the relations of the further developed external and internal glomerulus.

b.c. body-cavity; c.v. cardinal vein; e.gl. external glomerulus; gl. glomerulus; i.c.m. intermediate cell-mass; i.gl. internal glomerulus; me. mesentery; p.f. peritoneal funnel; W.d. Wolffian duct.

(1) The now hollow Wolffian duct; (2) the outgrowth from it to the intermediate cell-mass forming the upper limb of the S; (3) the intermediate cell-mass with the commencing lumen from the body-cavity.

At a slightly later stage (fig. 177, A—C) there is a distinct lumen opening into the body-cavity, which is continued behind into the part of the intermediate cell-mass which has separated from the peritoneal epithelium (C, *i.c.m.*). This part will in the next stage (fig. 177, E) become converted into that part of a tubule in which a Malpighian body is developed, while the anterior part will form a much wider peritoneal funnel (nephrostome).

A glomerulus is formed about this time on the anterior wall of the peritoneal funnel of each segmental tubule. The glomerulus increases in size, and its lower portion hangs down freely into the body-cavity (fig. 177, F, *gd*). Before the period of the greatest development of the glomerulus the mouth of the peritoneal funnel becomes closed, thus dividing the glomerulus into an anterior lower or external portion and into a posterior upper or internal portion, the latter persists as the glomerulus of the Malpighian body of the Wolffian body. The external portion afterwards disappears.

Behind the fifteenth segment the segmental tubules develop entirely from the cells of the intermediate cell-mass. At first the intermediate cell-mass is at points distinctly continuous with the peritoneal epithelium; at others it is less so. It soon breaks away and occurs as a solid cord of cells, connected at intervals with the peritoneal epithelium.

At the next stage the intermediate cell-mass entirely breaks away from the peritoneal epithelium, and lies as a cellular blastema (the Wolffian blastema) just internal to the Wolffian duct. The Wolffian blastema almost directly breaks up into the structures constituting the first rudiments of the Wolffian tubules.

Posteriorly, from about the twentieth segment, the intermediate cell-mass has never any connection with the peritoneal epithelium, and gives rise to the Wolffian blastema quite independently of the peritoneal epithelium.

The cells of the blastema group themselves into tubules, one end of which forms the Malpighian body, and the other opens into the Wolffian duct. There appear to be outgrowths from the duct to meet the tubules.

Although the Wolffian blastema extends as far back as the thirty-fourth segment, it does not break up into Wolffian tubules behind the thirtieth segment. From the thirty-first to the thirty-fourth segment it undergoes a different fate, and is known as the kidney blastema.

In the anterior region of the mesonephros there appears to be only one primary tubule (Wolffian tubule) for each segment of the body, but the number increases up to the twentieth (counting from the auditory involution). All the segments from the twentieth to the thirtieth inclusive contain five or six primary tubules.

The secondary or dorsal tubules are also more numerous behind than in front, the most anterior segment being about the twenty-first. Some primary tubules, according to Sedgwick, have as many as four secondary tubules; thus in the twenty-eighth segment there are twenty secondary tubules (five sets of four).

Balfour has shown that the secondary tubules develop in *Elasmobranchs* in con-

nection with the Malpighian bodies of the primary tubules. A process from one Malpighian body grows forward and unites with the preceding tubule just before it enters into the Wolffian duct. The stalk of origin degrades into a fibrous band or is aborted. The tertiary, &c., tubules probably arise from the same rudiment.

The secondary Malpighian body is produced in the Fowl, according to Sedgwick, by the division of the primary glomerulus into two parts, the upper one forming the secondary and the lower the primary glomerulus; and by the simultaneous development of certain folds which separates the dorsal secondary tubule from the ventral primary tubule.

The somewhat later origin of the posterior tubules of the mesonephros in the Fowl, and their development from a blastema, is a distinct approach towards the mode of origin of the metanephros, now to be described.

It appears to be probable that in the Teleosts and Amphibia the segmental tubules of the mesonephros develop *in situ* from a blastema analogous to that in the posterior region of the Fowl. The tubules subsequently acquire openings into the Wolffian tube on the one hand, and into the body-cavity on the other.

3. **Metanephros.**—The kidney proper or metanephros, as a gland distinct from the mesonephros, only occurs in Amniota. In the Fowl it develops from a blastema which is at first perfectly continuous with, and indistinguishable from, that which gives rise to the posterior portion of the Wolffian body. Although the kidney blastema arises at a comparatively early stage in development, still it is not till a much later stage that it shifts its position and begins to show signs of developing into the segmental tubules. This retarded development is analogous with the late appearance in Amphibia of the mesonephros as compared with the pronephros.

The first distinct structure to develop is the ureter, which arises as a dorsal outgrowth from the hinder part of the Wolffian duct. The ureter grows forward in close connection with the above-mentioned blastema, which has by this time broken away from the mesonephric blastema and assumed a position dorsal to it (fig. 178, c).

The metanephric blastema extends in the Fowl from the thirty-first to the thirty-fourth segments, and collects round swellings of the ureter from which kidney tubules grow out. These tubules burrow into the blastema, and they are increased by segregation of the blastema cells.

The ureter soon loses its connection with the Wolffian duct, and acquires an independent opening into the cloaca.

The primitive continuity of the metanephric with the mesonephric

blastema, together with the general similarity of the development of the renal tubules and the identity of their adult structure, proves that the metanephros is merely a special portion of the primitive Wolffian body, which develops late.

The acquisition by the posterior portion of the Wolffian body in some Elasmobranchs and Amphibia of efferent ducts opening into

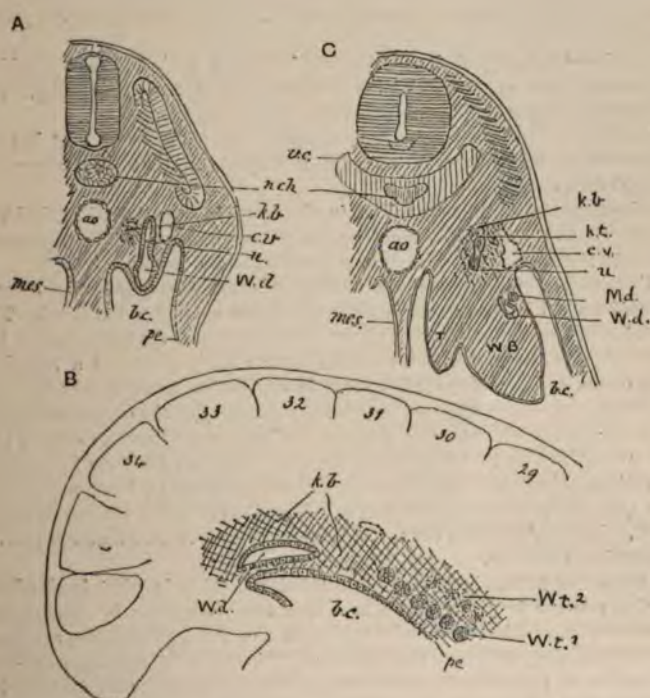


FIG. 178.—DEVELOPMENT OF METANEPHROS IN THE FOWL. [Adapted from Sedgwick.]

A. Transverse section through an embryo at the end of the fourth day. B. Longitudinal vertical section through an embryo of about the same age, showing the absolute continuity of the kidney blastema with the hindermost part of the Wolffian blastema, in which the development of Wolffian tubules is taking place. C. Transverse section through an embryo at the end of the sixth day.

ao, dorsal aorta; b.c. body-cavity; c.v. cardinal vein; k.b. kidney blastema; k.t. kidney tubule; M.d. Müllerian duct; mes. mesentery; nch. notochord; pe. peritoneum; T. testis; u. ureter; v.c. vertebral centrum; W.B. Wolffian body; W.d. Wolffian duct; W.t.¹ primary, and W.t.² secondary, Wolffian tubule.

the urogenital sinus or into the extreme posterior end of the Wolffian duct, is, as Balfour pointed out, a definite step towards the formation of a metanephros. According to Mikalovics, the mesonephros remains functional till the second year in Lizards, and thus is functional at the same time as the metanephros.

Summary of the Development of the Vertebrate Excretory Organ.—From his investigations on the development and phylogeny of the vertebrate excretory organs, Sedgwick has arrived at the following conclusions. For the facts and arguments upon which they are based, recourse must be had to his papers.

The pronephros attains a functional development in all the Ichthyopsida (except the Elasmobranchii), but usually only during larval life.

The segmental duct arises first as a ridge from the parietal peritoneum. This ridge usually contains a diverticulum from the body-cavity, and is continuously constricted off to form a duct.

Except anteriorly, where the constriction only takes place at intervals, leaving the openings of the pronephros (except in Teleostei, where there is only one opening).

These openings correspond in number with the segments which the pronephros occupies.

A vascular structure, called a glomerulus, is formed, projecting on each side of the aorta into a special dilatation of the anterior part of the body-cavity. (*Myxine* forms a peculiar exception to this otherwise universal fact.)

This dilated part of the body-cavity may become partially or completely separated off to form a capsule, into which the glomerulus projects and the anterior end of the segmental duct opens.

The development of the pronephros in the Fowl is essentially identical with the above, except in the absence of a continuous glomerulus opposite the nephrostomata; but that in the Elasmobranch is greatly modified and reduced.

In those animals which possess a functional larval pronephros, the mesonephros develops from a blastema; this is undoubtedly an abbreviated method. The lateness and consequent modification of the development of the mesonephros in these Ichthyopsida is due to the fact that the larva already possessed a functional excretory organ, and devoting all its energy in developing those organs which it will really require as a larva, it leaves over the development of the organs not so required until later; and in order that it may not be burdened by useless organs, the cells, which will give rise to the tubules, are so reduced as hitherto to have escaped observation. If the phylogenetic order had been adhered to, these cells would have arisen quite early in embryonic life, and from the parietal mesoblast in the normal manner. In the Amphibia the mesonephros increases in size and complexity with the growth of the larva.

On the other hand, the mesonephric tubules develop in what is clearly a more primitive manner in those forms in which the pronephros is functionless. In Elasmobranchs, and in the anterior region in the Fowl, the tubules are practically persistent tubular portions of the body-cavity (since the intermediate cell-mass is a continuation of the coelomic epithelium), which soon acquire an opening into the segmental duct. The early discontinuity of the tubules with the duct is, however, a secondary feature. In Birds a segmental glomerulus is developed in connection with each nephrostome, part of which is converted into the glomerulus of the Malpighian body. In Elasmobranchs only internal Malpighian bodies are formed.

It may fairly be assumed that the Wolffian tubules were primitively segmentally arranged (as still occurs in the development of Elasmobranchs, *Cæcilia*, and at first also in the Lizard). A shifting of position has, however, occurred, probably partly owing to the shortening up of the organ, so that the number of tubules may exceed that of the segments over which the mesonephros extends. The number of tubules in a segment usually increases with the growth of the embryo, and at the same time the organ is complicated by the development of secondary tubules.

In Birds the pronephros is continuous with the mesonephros. The discontinuity in Amphibia is due to the causes mentioned above, but it may not really be so great as it appears.

The segmental tubules of the Ichthyopsidan pronephros open into a special recess of the body-cavity, into which the elongated glomerulus projects (fig. 173); imme-

diately above this lies the muscle-plate. A comparison of figs. 173-177, will demonstrate that the intermediate cell-mass corresponds to this region. It has been shown that in Birds the peritoneal funnels, the Malpighian body, and a portion at least of the mesonephric tubules are derived from the intermediate cell-mass. The external and internal glomeruli of the Avian Wolffian body are developed from the same region, and all the secondary glomeruli are derived from the internal glomerulus. The internal glomeruli of Elasmobranchs are clearly homologous with those of Birds. According to this view, a Malpighian body is to be regarded as an isolated portion of the body-cavity, comparable with the condition which obtains in the Teleostean pronephros. Therefore the mesonephros, in all particulars, is merely a continuation posteriorly of the primitive vertebrate excretory organ, which, for various reasons, has acquired a more or less independent and modified origin.

What applies to the mesonephros also holds good for the metanephros. The distinction of the latter organ from the former is more apparent than real, as Sedgwick has fully demonstrated. As a matter of fact, the tubules of the hindermost region of the mesonephros develop in an almost similar manner to those of the metanephros. We have therefore a complete series in the mode of origin of the excretory tubules, from the primitive condition in the pronephros of Amphibia to the modified method by the rearrangement of the cells of a blastema, as occurs in the metanephros of Amniotes.

From the foregoing brief summary it will be seen that the excretory organs of the adult are usually developed from the walls of the body-cavity in the invertebrate and vertebrate Coelomata (and therefore the same possibly occurred in the lower Chordata). It must not, however, be rashly concluded that these organs are necessarily homologous. It is possible that a similar and homologous simple renal organ (archinephridium) occurred in the unsegmented vermian ancestors of the Chaetopoda and Chordata; but the segmental organs of the one are probably homoplastic, rather than strictly homologous with the segmental tubules of the other.

It is tempting to regard the origin of the Nemertean excretory organ, as described by Hubrecht, as a degenerate form of the production of a true body-cavity (coelom) by archenteric diverticula, which, in this case, solely develop into nephridia. If this be granted, a further step may be taken, and, accepting Rabl's account of the development of the Molluscan excretory organ, we may assume that the formative cells of the mesoblastic vesicle actually arose from the archenteron. Should this prove to be the case, the Molluscan nephridia would be comparable with those of the majority of other animals. It is also difficult to believe that the Molluscan pericardium is not a true coelomic cavity.

Epiblastic Origin of the Segmental Duct.—Since the above account of the development of the vertebrate excretory septum was in type, a preliminary note by Von Perényi has appeared, in which he confirms and extends the discovery of the epiblastic origin of the segmental (archinephric) duct. Hensen, Graf Spee, and Flemming have demonstrated that in the Rabbit and Guinea-pig the primitive nephric duct (probably not the whole excretory system, as they assume, although without evidence to support them) arises by delamination from the epiblast at the level of the intermediate cell-mass, with which it later becomes associated. Afterwards Van Wijhe found the same held good for Elasmobranchs, and most recently Von Perényi asserts that in the Edible Frog the segmental

duct develops as a canal-like splitting from the inner (nervous) cell layer of the epiblast, and quite close to the place of origin of the developing somites. In the Lizard, also, it appears as a thick cell-mass separating off from the epiblast.

There can now be little doubt that the segmental duct arises from the epiblast. This discovery will necessarily lead to a modification of our views concerning the morphology of the vertebrate excretory organs.

The segmental tubules (nephridia) appear to be strictly mesoblastic, and the above account of their development may be taken as probably being fairly accurate. The origin of these nephridia may have been primitively similar to those (segmental organs) of the Chaetopod Worms, the main distinction between the two being that each nephridium of the latter opens directly to the exterior. As has been already stated, Hatschek has described a single nephridium in *Amphioxus* in all respects comparable with a vermician nephridium.

We have, then, only to assume that a pair of similar vermician nephridia occurred in each body-segment of the ancestral Vertebrate, and that the nephridia of each side of the body opened externally into a lateral groove. It would further only be



FIG. 178*. TRANSVERSE SECTION OF EMBRYO RABBIT (4 mm. in length, stage of sixteen somites). [After Flemming.]

The section is taken just in front of the posterior termination of the intestine. The right side of the figure is the left of the body. There is a small rupture in the left (right of figure) mesoblastic somite. All the shading is diagrammatic.
al. mesenteron (intestine); *ca.* coelom (body-cavity); *ep.* epiblast; *ay.* hypoblast; *i.c.m.* intermediate cell mass; *n.c.* neural canal; *s.d.* segmental duct; *som.* somatic mesoblast; *sp.* splanchnic mesoblast.

necessary for the groove to deepen and next to form a canal (in the same manner that the neural groove is converted into a canal) to bring about the vertebrate arrangement. Thus in Vertebrates, as in Invertebrates, the nephridia open by epiblastic pores, but in the former the area upon which they open is precociously converted into a canal, which subsequently acquires a secondary opening to the exterior through the cloaca.

As we are justified in assuming the persistence of the blastopore as the anus in early Chordata, the nephric groove, if it were continued behind round to the anus, would practically open into the extreme hinder end of the mesenteron—in other words, into the urodæum. Probably about the same time that the nephric groove was being converted into the nephric canal (segmental duct), the proctodæum was being invaginated. The latter would push before it the posterior orifice of the nephric canal along with the primitive anus (blastopore). On the hypothesis just sketched out, the nephridia of Vertebrates always open by their original epiblastic pores, primitively directly to the exterior, secondarily into a canal separated from the epiblast; also the archinephros could be equally effectually functional throughout the whole period of its modification.

Urogenital Ducts of Vertebrates.—For the sake of simplicity the ducts of the Vertebrate renal organs have been referred to as if

solely connected with those organs; as a matter of fact, they become intimately connected with the generative organs. The modifications which occur in the glands and ducts of the primitive excretory system of the Vertebrates may be regarded as being largely due to their secondary connection with the generative organs.

Segmental or Archinephric Duct.—The development of the segmental duct has already been described. For the sake of clearness it has been assumed that the segmental duct functions first as the duct of the pronephros, and secondly as that of the mesonephros. This is not, however, exactly the case, as in most cases there is a horizontal division or separation of the duct into two tubes. A ventral tube is termed the Müllerian duct; while the dorsal, from its association with the mesonephros, is known as the mesonephric or Wolffian duct.

Müllerian Duct.—The two ducts are formed in Elasmobranchs by the splitting off from before backwards of a nearly solid cord of cells from the ventral wall of the segmental duct. A very small portion of the lumen of the segmental duct may perhaps be continued into the Müllerian duct. The latter soon grows in size, and forms an elongated tube in the female quite distinct from the Wolffian duct. The longitudinal separation from the segmental duct occurs in such a manner that the whole of the anterior extremity, with its peritoneal opening, belongs to the Müllerian duct, which now forms a complete tube opening posteriorly into the cloaca and anteriorly into the body-cavity. In these forms the single, primitively solid, pronephric tubule persists as the peritoneal opening of the Müllerian or oviduct of the adult.

The development of the Müllerian duct in Amphibia is very much the same as in Elasmobranchs. In the Salamander the Müllerian duct is split off from the segmental duct behind its anterior extremity, and acquires an independent opening into the body-cavity slightly behind the pronephros. Unlike what occurs in Elasmobranchs, the undivided anterior extremity of the segmental duct with the pronephros retains its connection with the Wolffian duct.

In the Fowl, Balfour and Sedgwick have shown that the anterior end of the Müllerian duct arises as three grooves connected by an internal thickening of the peritoneum of that region. The thickening separates as a solid rod of cells, which, before long, acquires a central lumen. The whole structure now consists of a short tube opening anteriorly into the body-cavity by three short ductules.

Posteriorly the Müllerian duct is closely connected with the segmental duct. The backward growth of the Müllerian duct takes place at the expense of a thickening of the ventral wall of the segmental duct. In other words, the avian Müllerian duct is formed posteriorly by the splitting of the segmental duct, as in Elasmobranchs and Amphibia. The permanent abdominal opening of the Müllerian duct (oviduct) corresponds with the anterior of the three grooves, the two posterior grooves disappearing.

Balfour regarded the three peritoneal funnels of the Müllerian duct as the sole representative of the head-kidney (pronephros) in the Fowl. Sedgwick still adheres to the earlier published view as to the meaning of the peculiar structures at the anterior end of the Müllerian duct, but supposes them to have been derived from the anterior part of the excretory system after its modification to form the pronephros.

The tubules of the Müllerian duct of the Fowl arise behind the anterior end of the segmental duct, and therefore more or less posterior to the pronephros. In Amphibia the single (solid) tubule is situated behind the pronephros. In both cases we must assume either that the Müllerian tubules are modified and backwardly-shifted pronephric tubules, or that they belong to the region between the pronephros and the mesonephros proper. In any case, the Müllerian duct is split off from the segmental duct. Further researches may modify the account given of the development of the pronephros of Elasmobranchs.

The Müllerian duct opens at the anterior end of the body-cavity in the lower Vertebrates; in Elasmobranchs, for instance, the conjoint orifice of the two ducts is situated on the ventral wall of the oesophagus just behind the pericardium. In the higher Vertebrates the Müllerian ducts are situated in the posterior abdominal region. The hydatid (fig. 181, A, *h*") which is sometimes present near the coelomic orifice of the oviduct is probably a degraded rudiment of a primitive tubule.

In those Ichthyopsida which possess them, in the Sauropsida and in the Ornithodelphia (Monotremata or Prototheria), the paired Müllerian ducts (oviducts) open into that portion of the cloaca which is known as the urogenital sinus (fig. 179, A). Occasionally only one oviduct may be developed; in Birds it is usually the right which atrophies.

The Didelphia (Marsupials or Metatheria) have a modification of their Müllerian ducts, which is very different from that of other Mammals. It may be here mentioned that three regions are distinguishable in the Müllerian ducts of these and higher Mammals—an anterior or distal narrow tube (Fallopian tube or "oviduct"), which opens into the body-cavity by usually fimbriated lips; a median swollen uterus, and a posterior or proximal vagina.

In the Didelphia the Müllerian ducts with their three regions are at first perfectly distinct, and practically remain so; that is, there are two vaginæ, uteri and Fallopian tubes. Later, in the young, the anterior (distal) ends of the vaginæ

approach one another; at the point where they touch they form a median sac, which grows backwardly towards the urogenital sinus. At first this vaginal cæcum is a double tube, corresponding to each vagina; but the median septum is usually soon absorbed. At this stage the two uteri open into the anterior extremity of the vaginal *cul-de-sac*, into the upper end of which the two vaginæ also open. The blind posterior end of the cæcum becomes closely connected with the end of the urogenital sinus, between the posterior vaginal orifices; and, as Fletcher has proved, the two cavities may communicate even in virgin animals, and they certainly do communicate after the first birth. (Unless very exceptionally, there is, according to Fletcher, no direct communication in *Macropus major* between the vaginal cæcum and the urogenital sinus, even after young have been produced.)

In the Monodelphia (Eutheria) the Müllerian ducts fuse with one another to an increasing extent from behind forwards. In

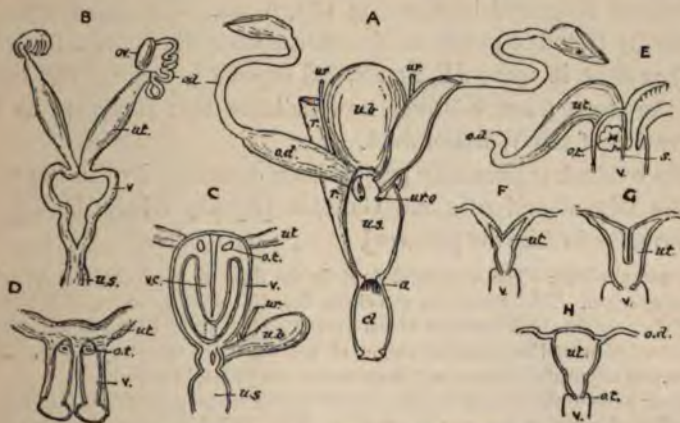


FIG. 179.—VARIOUS FORMS OF MAMMALIAN UTERI.

A. *Ornithorhynchus* [after Owen]. B. *Didelphys dorsigera* [after Brass]. C. *Phalanger vulpina* [after Brass]. D. Double uterus and vagina; Human anomaly [after Ferris]. E. *Lepus cyniculus* (Rabbit), uterus duplex [after T. J. Parker]. F. Uterus bicornis. G. Uterus bipartitus. H. Uterus simplex (Human). [P-H after Wiedersheim.]

a. anus; c. cloaca; o.d. oviduct; o.t. os tincte (os uteri); ov. ovary; r. rectum; s. vaginal septum; u.b. urinary bladder; ur. ureter; ur.o. orifice of same; u.s. urogenital sinus; w. uterus; v. vagina; v.c. vaginal cecum.

all there is a single vagina, but in some of the lower forms, *e.g.*, Rodents, an imperfect vaginal septum may be present. Usually it merely divides the orifice (os uteri or os tincæ) of one uterus from that of the other (fig. 179, E). In such forms the uteri are quite distinct.

In other Mammals the uteri come together, and by concrescence form a common uterus, which also, in some cases, possesses a short median septum. In these forms there are paired cornua uteri opening into a single corpus uteri, which communicates with the vagina by a single os uteri.

Fig. 179 illustrates various forms of uterus met with amongst

the Eutheria. In the most specialised case, as in Man, the uterus (*H, ut*) has a pyriform shape, and the Fallopian tubes arise abruptly from its anterior corners.

It is interesting to find that anomalies may occur in the human uterus, which illustrate the evolution of that organ. Thus a median septum may partially or wholly extend along the uterus, and the vagina even may be similarly divided (fig. 179, D).

The Müllerian duct is rudimentary or entirely absent in the adult male. In the former case it may be represented by a solid cord for the whole of its length (Dipnoi and some Amphibia, fig. 180, A, *mg*), or only the anterior portion may remain (Elasmo-branchs and some Lizards), which degrades into the so-called hydatid of Morgagni in Man (fig. 181, B, *m*). The posterior section is usually stated to persist as the uterus masculinus (figs. 183, III, *u*, 184), present in many Mammals, and especially large in the Rabbit and the Horse; but Kölliker now believes this structure to be a derivative of the Wolffian duct.

The oviduct is normally present as a complete duct in the males of the Dipnoi and of some Ganoids [Ayers, Wiedersheim], and abnormally in Lizards [Howes].

To recapitulate:—The segmental duct is the duct of the primitive vertebrate excretory organ. The pronephros was either the sole excretory organ, or it has come to be the only functional portion of the kidney in free-living larval forms, owing to the retardation of the posterior region of the primitive excretory organ. At all events, the segmental duct at first functions as the pronephric duct.

One or more of the tubules in the anterior region of the primitive kidney acquired the office of carrying ova to the exterior. This probably occurred after the full development of the pronephros, and in the intermediate region between it and the mesonephros. Possibly at one time the segmental duct conveyed ova to the exterior, together with secretions from both pronephros and mesonephros.

From certain causes the pronephros atrophied or changed its function and became a lymphatic gland; the segmental tube then carried ova and mesonephric secretions. The duct gradually became constricted in such a manner that the ova were conveyed in a ventral groove, which subsequently was converted into a canal.

In some such manner the segmental duct may have differentiated into a ventral Müllerian duct or oviduct, and into a dorsal mesonephric duct or Wolffian duct.

Wolffian Duct or Mesonephric Duct.—In those forms (Ichthyopsida) in which the mesonephros remains functional throughout life its duct naturally persists, although it also acts as the efferent duct of the generative gland in the males of the Elasmobranchii, Lepidosteus, and Amphibia.

Branches grow out from the anterior (three or four in Elasmobranchs) segmental or Wolffian tubules (though probably not from their peritoneal openings—Balfour) and enter the testis, where they form a longitudinal canal (fig. 180, A). These branches, vasa

efferentia, convey the semen to the Wolffian body after previous uniting into a longitudinal canal, (the longitudinal canal of the Wolffian body) (fig. 180). Branches of this so-called testicular

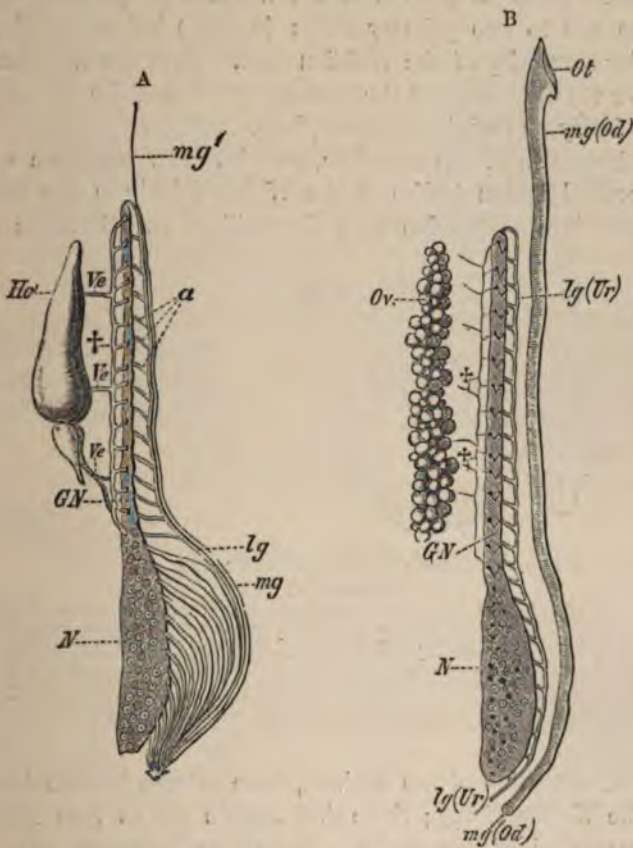


FIG. 180.—DIAGRAM OF THE UROGENITAL APPARATUS OF A MALE (A) AND FEMALE (B) URODELE. Founded on *Triton taeniatus*. [From Wiedersheim after J. W. Spengel.]

a. collecting tubules of the mesonephros; GN. anterior sexual portion of kidney (parorchis of the male); Ho. testis; lg. Wolffian or Leydig's duct, urogenital duct in male, A, and urinary duct in female, B, Ur; mg(Od). Müllerian duct, rudimentary in male, mg; N. posterior non-sexual portion of kidney; Ot. peritoneal aperture of oviduct; Ov. ovary; Ve. vasa efferentia of testis which fall into the longitudinal canal (tt) of the Wolffian body; this testicular network (tt) is rudimentary in the female, B.

network enter certain Malpighian bodies, and the semen is thence carried by their tubules to the Wolffian duct.

The anterior or sexual portion of the Wolffian body in the male is rudimentary so far as excretory purposes are concerned, and, as in the male, a functionless rudiment of the Müllerian duct is present, so a rudimentary testicular network is developed in the

female Urodeles (fig. 180, B), and the anterior portion of the Wolfian body is also feebly developed.

In the Elasmobranchs and Amphibia the collecting tubes of the non-sexual posterior portion of the Wolfian body unite together to form one to two primary tubes (ureters) before entering the posterior extremity of the Wolfian duct. Thus the Wolfian tube acts as a vas deferens, and the posterior portion of the mesonephros is practically an incipient metanephros.

In the males of the Amniota, tubules grow out from certain anterior Malpighian bodies of the Wolfian body in the embryo, and come into connection with the seminal tubuli of the testis.



FIG. 181.—GENERATIVE ORGANS OF HUMAN ADULT. [After Kobelt.]

A. Female. B. Male.

The Müllerian duct (*M*) in the female functions as the oviduct or Fallopian tube; from below its fimbriated abdominal opening is seen an hydatid, probably the rudiment of a pronephric tubule; in the male the blind end of the Müllerian duct forms the hydatid of Morgagni, *m*. The Wolffian body persists in three sections—(1.) the anterior as rudimentary tubes, sometimes forming hydatids, *h*; *K*, terminal bulb or hydatid in female; (2.) the middle set of tubes (*c*) or coni vasculosi, forming the epididymis of the male and the epoophoron of the female, *ep*; (3.) the posterior rudimentary tubules, paroophoron of female and vasa aberrantia of male. The fold of mesentery slinging the ovary (*o*) is the mesorchium; *t*, testis.

With the exception of two or three, these tubules become detached from the Wolfian body; those that remain act as vasa efferentia (coni vasculosi of Mammals). Several rudimentary outgrowths from the Malpighian bodies may persist as hydatids or as vasa aberrantia (fig. 181, B, *v.a*).

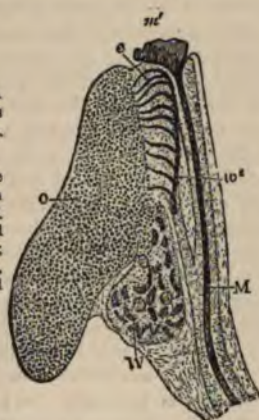
The Wolfian duct in the male Amniota is transformed into the vas deferens; its anterior portion becomes extremely convoluted, and forms the canal of the epididymis, the head of the epididymis being formed from the testicular network, which, as has just been described, is secondarily developed from the Malpighian bodies.

In the female rudimentary structures of a similar nature occur (figs. 181, A, *h*, *v.a*); the anterior tubules form hydatids, the posterior degenerate into solid cords. These structures are collectively known as the paroovarium (epoophoron or Rosenmüller's organ).

The Wolffian duct more or less disappears in the female. In Snakes and several Lizards the posterior portion may remain as a small functionless canal, and in some Mammals (Pig, Ruminants.

FIG. 182.—UROGENITAL ORGANS OF A FEMALE HUMAN FETUS OF $3\frac{1}{2}$ INCHES LONG, OR ABOUT FOURTEEN WEEKS. [From Quain after Waldeyer.]

e. tubes of the anterior part of the Wolffian body, forming the epoophoron of Waldeyer (parovarium of Kobelt); *M.* Müllerian duct; *m.* its anterior fimbriated orifice; *o.* ovary full of primordial ova; *W.* posterior part of the Wolffian body, forming the paroophoron of His and Waldeyer; *w.* Wolffian duct.



Fox, Cat, and some Monkeys) the middle portion may persist as Gaertner's duct.

The posterior or non-sexual portion of the Wolffian body de-

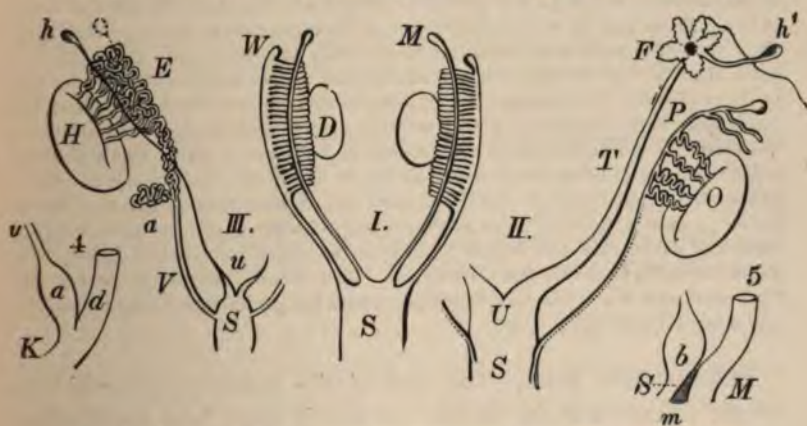


FIG. 183.—DIAGRAMS REPRESENTING THE RELATIONS OF THE UROGENITAL ORGANS IN THE MALE AND FEMALE EUTHERIA. [From Landois and Stirling.]

I. Ideal undifferentiated condition.—*D.* reproductive gland lying on the tubules of the Wolffian body, *W.*; *M.* Müllerian duct; *S.* urogenital sinus. II. Transformations in the female.—*F.* fimbriated orifice, with hydatid (*h'*) of the Fallopian tube, *T.*; *O.* ovary; *P.* parovarium; *U.* uterus. III. Transformations in the male.—*a.* vas aberrans; *E.* epididymis with hydatid, *h.*; *u.* uterus masculinus; *V.* vas deferens; *S.* urogenital sinus. 4. Monotrematous, and 5. Eutherian, stages in development of the posterior passages.—*a.* allantois; *b.* bladder; *u.* urachus; *d.* and *M.* rectum; *k.* cloaca; *S.* urogenital sinus; *m.* perineum.

grades into the para-epididymis or organ of Giraldès in the male (fig. 184, *w.*), and into the paroophoron in the female (fig. 185, *w.*).

R

Generative Ducts of Ganoids and Teleosts.—There are not at present sufficient data upon which to satisfactorily determine the homology of the Teleostean oviduct. Rathke, Balfour, and Huxley have demonstrated that the Teleostei form an extreme of the Ganoid series, and that the oviduct of the Smelt (*Osmerus*) is in every way identical with that of *Amia*. Some Teleosts, such as the Salmon, have no oviduct, their ova dehiscing into the body-cavity to pass to the exterior through the abdominal pore. Huxley points out that in the Sturgeons (*Sturios*) and *Lepidosteus* the renal are much wider than the generative ducts, and the communication between them is effected far in front of the external aperture; while in *Polypterus* and *Amia* the oviducts are wider than the ureters, and they communicate nearer the external opening; in *Osmerus* the common aperture of the oviducts lies in front of the opening of the ureter; and lastly, in the *Salmo* the abortion of the oviducts, commenced in *Osmerus*, is completed, and the so-called "abdominal pore" is the homologue of half of the urogenital opening of the Ganoids, and has nothing to do with the "abdominal pores" of these fish and of the Selachians. Against this view must be placed the fact, discovered by Rathke and confirmed by Bridge, that in *Mormyrus oxyrhynchus* the ordinary generative ducts coexist with abdominal pores. There is, unfortunately, no complete account of the development of the Ganoid oviduct; it is possible that it represents, in part at least, the Müllerian duct of other forms, but Balfour has suggested that it is a modified segmental tubule of the mesonephros.

There is also great uncertainty concerning the nature of the duct of the testis in Teleosts. What has been said above for the oviduct also applies largely to the efferent duct of the testis. Balfour has proved that the anterior portion of the Wolffian body in *Lepidosteus* is connected with the testis as in *Elasmobranchia*, and thus in that Ganoid the Wolffian duct functions as the vas deferens.

Weber, who has very recently investigated the subject, has come to the conclusion that the genital pore in female Salmonidæ is the homologue of that of other Teleostei; it communicates with a pair of peritoneal funnels which open widely into the body-cavity. These may in some instances extend forwards close to the ovary (*Mallotus*, *Osmerus*). The peritoneal funnels are incompletely homologous with the oviducts of those Teleostei with so-called enclosed ovaries, and neither are homologous with the oviducts of other Vertebrates. In the male Salmonidæ the vasa deferentia of the testes open to the exterior by a pore common to the ureters, precisely as in other Teleostei. In old Salmonids, in males as well as in females, a pair of true abdominal pores occur, a pore being situated on each side of the anus. They are not concerned in the evacuation of ova; in individual cases one or both may be absent. Weber considers these abdominal pores as rudimentary structures, perhaps as remnants of segmental ducts. He homologises them with the abdominal pores of *Holocephali*, *Elasmobranchii*, *Ganoidi*, and *Mormyridæ*. The so-called abdominal pore of the *Cyclostomi* and *Muraenidæ* may be compared with the genital pore of the Salmonidæ and other Teleostei (*cf.* p. 214).

Metanephric Duct.—The duct of the metanephros or kidney proper is known as the ureter. At first it opens into the Wolffian duct, but it early acquires an independent opening into the cloaca (urogenital sinus).

In *Sauropsida* and *Monotremes* the ureters open into the urogenital sinus quite independently of the urinary bladder. In the higher *Mammals* the ureters open directly into the bladder.

Suprarenal Bodies.—The suprarenal bodies of Vertebrates were shown by Balfour to have a double origin. The medullary substance is derived from an extension of

the ganglia of the sympathetic system, while the cortical substance is of mesoblastic origin.

Weldon has lately demonstrated that the cortical substance of the suprarenal bodies arises as a proliferation of the peritoneum, just internal to the segmental tubules, throughout the whole extent of the mesonephros. This blastema subsequently surrounds the outgrowths from the ganglia.

In *Bdellostoma*, as Weldon has shown, the head-kidney has become modified so as to form an organ functionally analogous to the suprarenals; while in Teleosts a most remarkable series of modifications, affecting every region of the kidney, has been described by Balfour and Emery.

Weldon holds that the same causes which led to the degeneration of the original renal pronephros (causes among which the specialisation of the pericardium and the development of the air-bladder and lungs may have played a considerable part), the same causes which led to the establishment of the mesonephros as the chief seat of renal secretion, may, and indeed must, have rendered advantageous the suppression of any glandular organ in the pronephric region; and thus when, in consequence of the change of function of the Wolffian duct more and more, the mesonephros became useless as a kidney, it is easy to understand how some of its component parts underwent in their turn the same change of function as had been undergone by the anterior part of the renal organ at an earlier period of its evolution.

Urinary Bladder.—A dilated portion of the Wolffian ducts which occurs in many Fishes is usually termed a urinary bladder. In Amphibia a thin-walled vesicle (urocyst) develops from the ventral wall of the cloacal section of the mesenteron, and is homologous with the urinary bladder of the Amniota. On referring to the mode of development of the Wolffian duct, it will be obvious that the piscine "urinary bladder" is not in any sense of the term homologous with that of the Amniota.

In the Amniota the urinary bladder is a persistent portion of the stalk of the allantois (p. 81), which becomes converted into a vesicle. That portion of the stem of the allantois distal to the bladder which remains within the body-cavity after the formation of the umbilical cord becomes degraded into a solid cord, and is known as the urachus (figs. 143, 184, 185).

The bladder opens on the ventral wall of the cloaca in Amphibia and in those Sauropsida in which it persists throughout life (*Chelonia* and *Lacertilia*). In these the ureters open independently into the cloaca.

In the Monotremes the bladder opens into the anterior end of the urogenital sinus (fig. 179, A, *u.s.*), into which the ureters and generative ducts also debouch. The urogenital sinus or vestibule may be regarded as the proximal portion of the allantoic stalk.

In all higher Mammals the ureters open directly into the bladder itself, owing to the increase in length of the primitively short interspace between the orifices of the ureters and generative

ducts. This narrow lengthened portion of the urogenital sinus is known as the urethra (fig. 184). The urethra and generative

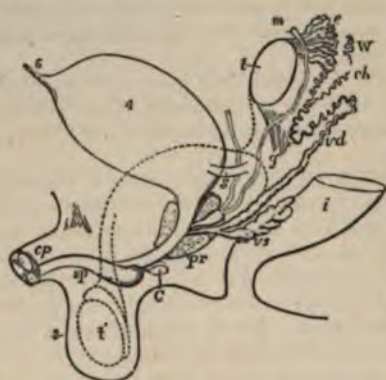


FIG. 184.—DIAGRAM OF THE MAMMALIAN TYPE OF MALE SEXUAL ORGANS. [From Quain.] Compare with fig. 185.

C. Cowper's gland of one side; cp. corpora cavernosa penis, cut short; e. caput epididymis; g. gubernaculum; r. rectum; m. hydatid of Morgagni, the persistent anterior end of the Müllerian duct, the conjoint posterior ends of which form the uterus masculinus; pr. prostate gland; s. scrotum; sp. corpus spongiosum urethrae; t. testis (testicle) in the place of its original formation, the dotted line indicates the direction in which the testis and epididymis change place in their descent from the abdomen into the scrotum; vd. vas deferens; va. vas aberrans; W. vesicula seminalis; W. remnants of Wolffian body (the organ of Giralde's or paradidymis of Waldeyer), 3, 4, 5, as in fig. 185.

ducts open into the anterior extremity of the urogenital sinus in Marsupials and many of the lower Eutheria (compare fig. 179).

This condition always persists in the male (fig. 184), as the urogenital sinus traverses the penis. In the females, however, of

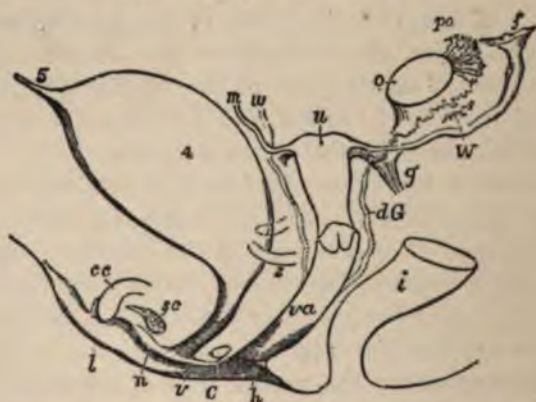


FIG. 185.—DIAGRAM OF THE MAMMALIAN TYPE OF FEMALE SEXUAL ORGANS. [From Quain.]

This diagram should be carefully compared with fig. 184, it will be seen that the dotted lines in one indicate functional organs in the other, and help to demonstrate the significance of certain rudimentary structures.

C. gland of Bartholin (Cowper's gland); c.c. corpus cavernosum clitoridis; dG. remains of the left Wolffian duct, which may persist as the duct of Gaertner; f. abdominal opening of left Fallopian tube; g. round ligament (corresponding to the gubernaculum); h. hymen; i. rectum; l. labium; m. cut Fallopian tube (oviduct or Müllerian duct) of the right side; n. nympha; o. left ovary; po. parovarium; sc. vascular bulb or corpus spongiosum; u. uterus; v. vulva; vd. vagina; W. scattered remains of Wolffian tubes (paroophoron); w. cut end of vanished right Wolffian duct; 3. ureter; 4. bladder passing below into the urethra; 5. urachus or remnant of stalk of allantois.

the more specialised Eutheria the urogenital sinus becomes much shortened and flattened out, so that eventually it is merely re-

presented by the space known as the vestibule of the vulva (fig. 185, 189). In the forms in which this occurs the urinary and generative ducts come to have independent openings to the exterior. The accompanying diagrams illustrate the changes undergone in the human female fetus.

At an early period (figs. 186 and 143, A) the allantois and Müllerian duct communicate with the rectum, but not with the exterior. The proctodæum is next developed (fig. 187), and forms a cloaca, into which the urogenital ducts and the rectum open. The cloaca is then divided into an anterior or ventral part, the urogeni-



Fig. 186.



Fig. 187.



Fig. 188.

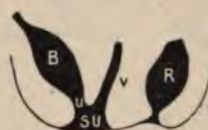


Fig. 189.

DIAGRAMS ILLUSTRATING THE EVOLUTION OF THE POSTERIOR PASSAGES.
[From Landolt and Stirling.]

Fig. 186.—Allantois continuous with rectum. Fig. 187.—Cloaca formed. Fig. 188.—Early condition in male, before the closure of the folds of the groove on the posterior side of the penis. Fig. 189.—Early female condition.
A, commencement of proctodæum; ALL, allantois; R, bladder; C, penis; CL, cloaca; M, Müllerian duct; R, rectum; U, urethra; S, vestibule; SU, urogenital sinus; V, vas deferens in fig. 188, vagina in fig. 189.

tal sinus, and into a posterior or dorsal portion, the anus (fig. 189), by a downgrowth of the tissue between the rectum and Müllerian duct, which forms the perineum. At a latter stage the bladder forms a rounded vesicle, and the urogenital sinus becomes much more shallow. Fig. 188 represents a stage in the male corresponding to fig. 190, B, before the urogenital orifice has become enclosed by the base of the raphé of the penis.

Mammalian External Generative Organs.—The external generative organs of the Eutheria develop as follows:—Anteriorly to the cloaca an elevation (genital eminence) appears, and surrounding it in front and on each side is a large cutaneous fold (fig. 190). The anus is next separated from the urogenital sinus by the formation of the perineum. The genital eminence grows rapidly, forming a cylinder, which is grooved on its posterior surface; the two folds of the groove extend back-

wards, so as to lie between the urogenital orifice and the large folds (fig. 190, B). So far the development is precisely the same for both sexes.

In the female the genital eminence usually remains comparatively small, and is known as the clitoris; its groove becomes less marked; the posterior edges of the groove persist as the nymphæ or labia minora. The anterior portion of the large cutaneous fold becomes the mons veneris, and the lateral folds greatly increase in size, so as, in most cases, to enclose the clitoris and constitute the labia majora.

In the male the genital eminence increases in size to form the penis. The margins of the groove close over, so as to convert it into a canal, the posterior ends at the same time growing over the urogenital orifice, so that the urogenital sinus is directly continued through the penis. The lateral portion of the large cutaneous fold unite together behind the penis, and fusing in the middle line, form the scrotum—the raphé indicating the line of junction. In some of the lower Mammals (*e.g.*, Rabbit) the scrotal sacs remain distinct. The so-called "urethra" of the male consists of three distinct regions: (1) the urethra proper, "prostatic portion," extending from the neck of the bladder to the orifices of the vasa deferentia and the uterus masculinus; (2) the urogenital sinus, "membranous portion;" and (3) the canal of the penis or "spongy portion."

On each side of the urogenital sinus corresponding to the large fold is a perforation of the inner wall of the abdomen, which is known as the internal inguinal ring. In

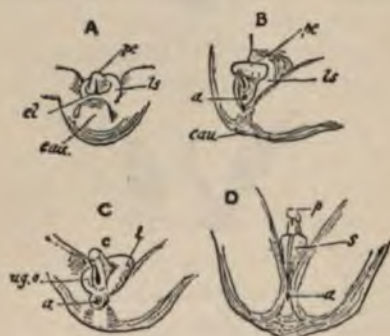


FIG. 190.—DEVELOPMENT OF THE EXTERNAL SEXUAL ORGANS IN THE HUMAN MALE AND FEMALE FROM THE UNDIFFERENTIATED CONDITION. [After Ecker.]

A. Embryo of about nine weeks, in which the external sexual distinction is not yet established and the cloaca still exists. B. An older embryo, without marked sexual distinction; the anus is now separated from the urogenital aperture. C. Female embryo of about ten weeks. D. Male embryo somewhat more advanced.

a. anus; cau. tail; c. clitoris; cl. cloaca; l. labium; ls. undifferentiated sexual fold; p. penis; p.c. undifferentiated sexual eminence; a. scrotum; u.g.o. urogenital opening.

the male a sac-like diverticulum of the peritoneum, the processus vaginalis, passes through the abdominal ring into the scrotum. In some Eutheria the testes always remain within the abdominal cavity, but in others they temporarily or permanently pass through the abdominal ring, and into the peritoneal pouch within the scrotum. Normally, in those animals in which a permanent descent of the testes occurs, the inguinal rings close, and the testes are enclosed within a serous sac; when this does not take place, a portion of the intestine may force its way through the ring into the scrotum, and thus produce a hernia.

Generative Organs.—The sexual cells are usually developed from a distinct epithelium; the Sponges form an apparent exception, as the sexual cells are derived from the mesenchymatous mesoderm, which is itself, however, probably solely derived from the endoderm.

Weismann and others have recently shown that, as a rule, the sexual cells arise from the endoderm of the stolon or stems of the fixed Hydroids, and subsequently migrate to what are termed the

generative organs. These latter may be situated within fixed (sporosacs) or detachable (medusoids) lateral buds or gonophores. The sexual cells mature in their secondary location. The sexual cells of *Hydra* are usually stated to be of ectodermic origin, but the prevalence of the former mode of origin in the marine Hydroids, combined with the fact of the presence of chlorophyll in the ovum of *Hydra viridis*, render it quite possible that a migration occurs also in this degraded fresh-water form.

In all the other Cœlenterates the ova and spermatozoa arise from the hypoblast of the mesenteric pouches or canals.

Lang states that in certain Turbellarian Worms (Polyclades) the sexual cells are developed at the expense of the epithelium of the gastric diverticula, that is, from the hypoblast.

Nothing definite is known concerning the development of the generative glands of Molluscs.

In *Sagitta*, although it belongs to the Cœlomata, a pair of primitive sexual cells appears as early as the gastrula stage, subsequently each cell develops into the ovary and testis of its side.

It is characteristic of most, if not of all the Cœlomata, that the generative organs arise from the epithelium of the body-cavity. There are no precise accounts of the mode of formation of the generative organs, or gonads, as they are more concisely termed by Lankester, amongst the Invertebrates. The structure of such organs is never complicated, and the dehiscence of free epithelial cells, as in the case of ova, is not specially remarkable.

The maturation of the ovum and its acquisition of food-yolk, and the difficult problem of spermatogenesis, have already been alluded to (p. 14).

In the Vertebrates the germ-cells are modifications of a special linear tract (germinal epithelium) of the peritoneum, between the mesonephros and the insertion of the mesentery (fig. 175, *p.o.*). The germinal epithelium may project more or less into the body-cavity to form a germinal ridge (fig. 178, *c.*).

It is now possible to make a general statement and affirm that in the great majority of cases, at least, the sexual cells arise from the endoderm (hypoblast) in the Acelomata; but in those forms in which the archenteron is produced into radial pouches, chambers, or canals, they occur on the walls of such diverticula.

In the Cœlomata the gonads are developed from the cœlomic epithelium; but as this is derived primitively from archenteric diverticula, the generative epithelium is practically a homologous tissue throughout the Metazoa.

The sexual products may find their way to the exterior by very different means. In some cases it is by the rupture or destruction

of the parent; they may migrate through the parental tissues, or dehisce into the body-cavity.

From the body-cavity they may pass to the exterior through abdominal pores (Cyclostomi and some Teleosts), or be conveyed by more or less modified nephridia (Chætopoda, Gephyrea, Brachiopoda, Mollusca, and some Vertebrates (see p. 237).

External generative or copulatory organs occur in the higher members of many groups, to render more certain the fertilisation of the ovum.

CHAPTER VIII.

GENERAL CONSIDERATIONS.

Complexity of Embryological Phenomena.—The phenomena of Embryology are of a very complex nature, owing to abbreviation or precociousness in the development of certain organs, and in the occurrence of a series of transformations which have reference solely to the ancestry of the individual, the latter often bearing no discernible relation whatever to the adult condition.

The irrelevance of these metamorphoses to the adult state is in some cases emphasised by the fact of their suppression in certain members of a group, as, for example, amongst the Scyphomedusæ. The genus *Pelagia*, although closely related to *Aurelia*, develops directly from the egg without the intervention of the Scyphistoma larva; and even *Aurelia* may abnormally have an abbreviated development. The characteristic larval forms of the Echinozoon Echinoderms are omitted in the development of those forms in which the young are reared in brood-pouches or similar protective chambers. The following will serve as types:—*Leptychaster kerguelensis*, *Ophiacantha vivipara*, *Hemiaster cavernosus*, and *Psolus ephippifer*. The direct development of *Astacus* is an example of the suppression of metamorphoses amongst the Crustacea, but in this Decapod a good deal of food-yolk is present.

The passing through of a free larval existence must be considered as constituting a drain upon the energy of the organism, and this loss naturally affects the adult condition. As Sollas points out, when such a larva "finally reaches the adult state, it has already to a considerable extent worn out its machinery and expended its powers of converting energy. A still more important consequence, however, would seem to follow from the premature aging due to a free larval existence, and that is the comparatively early exhaustion of the power of undergoing transformational change; the adult or comparatively stable state is reached sooner than it otherwise would be, and the chances of further development are

correspondingly diminished." It has been pointed out by several authors that the individual which is best equipped as an adult is that which has rapidly passed through its embryonic condition under circumstances where it has been extraneously nourished and protected. Again, to quote from Sollas, "The longer life in the mature state, acquired by those forms which are saved from the drudgery of a larval existence, offers increased opportunities for evolution to the adult animals, so that a progressive development, starting from higher and higher platforms, is directly favoured. But not only is a longer existence assured to the adult—existence in the embryonic state is shortened; and perhaps here the influence of seclusion is most clearly exhibited, for the energy which would be expended in a free larva in activities other than those involved in producing structural change is here solely devoted to that end, and hence the embryonic stages are passed over by secluded forms with comparative rapidity."

In studying the development of animals, it must always be remembered that what is known as the "struggle for existence" is continually acting upon the larval form as an individual, and that while the larva has to adapt itself to present conditions and to supply its own wants, the rudiments, or the formative tissue (blastema), of future organs may be precociously formed. This is the main reason for the complications and abbreviations which occur so frequently in the development of animals. Occasionally larval forms, so to speak, run wild, and do not develop into their normal adults, the form known as *Leptocephalus* amongst Teleosts affording a good example of this vagary.

The real nature of many embryological phenomena must remain unknown until the properties of protoplasm are considerably more elucidated. At present, we can deal only with the results, and not with the causes of changes in organic matter.

In the course of this work attempts have been made to indicate how certain organs may have been developed from pre-existing simpler structures in response to definite stimuli or to the requirements of the organism. The further our knowledge extends the more certain it appears that evolution is mainly the result of a mechanical necessity, or, as James Hinton put it, "organic forms are the result of motion in the direction of least resistance."

Suggestions as to the possible significance of observed embryological facts must be held only in the most tentative manner. It is easy to frame plausible theories respecting the evolution of

organs or of the animals themselves, but great caution is necessary in accepting them, and, at best, they should be regarded as merely working hypotheses.

Sketch of a Possible Evolution of the Metazoa.—The Protozoa combine all the essential activities of life within the limits of small independent units of protoplasm, and even in these differentiation may occur to a considerable extent. Those causes which result in the production of complicated organs in the Metazoa also act on unicellular forms, but, having less scope, the result is less evident. The higher organisation of multicellular animals is solely attributable to the large number of aggregated units which constitute their body; the forces acting upon all living beings must be the same.

The formation of masses or colonies of cells (aggregates of protoplasmic units) may possibly be primarily due to imperfect fission. Cell-division itself (*i.e.*, reproduction) is usually regarded as being primitively due to excess of growth consequent upon excess of nutrition; Geddes, however, suggests a different interpretation of the origin of cell-division (p. 279). Amongst the Protozoa reproduction results in the formation of distinct and independent organisms, each one of which is unicellular like its parent. In only a few forms are individuals aggregated into colonies, and in these but little co-ordination occurs.

More precise histological research is now demonstrating that in most, if not in all, animal (and vegetable) tissues the component cells are united together by strands of protoplasm, often of extreme tenuity. There may thus be a protoplasmic continuity extending throughout the whole organism, and possibly all the living cells of an animal are directly or indirectly connected with one another, except the lymph and blood-corpuscles.

The observations of Sedgwick on the syncytial segmentation of *Peripatus* (fig. 19) are in this respect very suggestive, and it may yet be proved that the complete division of an ovum into distinct segmentation spheres (fig. 12) is apparent rather than real.

It appears that all the cells of adult Coelenterates are connected together by means of protoplasmic processes, and it might fairly be assumed that the cells of a segmented coelenterate ovum and of the embryo into which it will develop are similarly united; but there is at present no definite embryological evidence to support this conclusion. The cellular network of the parenchymula larva

of *Obelia* (fig. 46) is, according to Merejkowsky, a secondary condition due to the fusion of the processes of amœboid cells.

Whether directly continuous or not, all the cells of a Metazoon are so grouped as to constitute a co-ordinated whole, the life of the individual being the sum-total of the activities or lives of the constituent cells. Theoretically each one of these cells possesses all the attributes of protoplasm, as, most probably, was actually the case when the ancestral form was passing from the Protozoon to the Metazoon condition, a stage which is now represented by the blastula larva. We may assume that each cell then possessed nutritive, sensory, metabolic, and reproductive functions; but in process of time specialisation occurred, and the concurrent limitation of function resulted.

In unicellular animals one pole or aspect of the body is usually concerned in the ingestion of food, and we are justified in assuming the same for the Protozoon ancestor of the Metazoa.

The segmentation of the ovum is stated to occur in two different ways. Either, according to the generally received account, it may from the first divide the cell horizontally into a nutritive (vegetative) and sensory (animal) portion; or, according to Agassiz and Whitman, the ovum may divide longitudinally (axially), then transversely, and lastly horizontally. In either case a multicellular mass is formed, of which the upper pole is more especially sensory (epiblast) and the lower nutritive (hypoblast). Assuming it to have been flattened, Bütschli has termed this theoretical ancestral form a *Plakula* (p. 23).

The series of stages from an unicellular form to an organism, consisting of two sets or layers of cells, presents us with no special difficulty, and plausible theories have been framed to account for the formation of a double-layered gastrula from the single-layered blastula. It is a matter of some importance to note that embryological evidence, as a whole, supports the conclusion that the future epiblastic (ectodermic) and hypoblastic (endodermic) cells are already practically differentiated in the blastula stage, and that the gastrula was evolved as a result of that differentiation. It is too often assumed that all the cells of the blastula are identical in every respect.

Brief History of Mesoblastic Tissues.—The conversion of a diploblastic form to one with three layers (triploblastic) is readily conceivable. It is possible that the third layer (mesoblast) primitively arose as the result of excessive nutrition of the nutritive

cells (hypoblast). The inner moieties of these cells separating themselves as amœboid cells (mesamœboids, or archæocytes of Sollas), which would then crawl about in the space (segmentation cavity) between the two layers. Similar cells arise in some embryos from the epiblast also. These cells would readily assume the amœboid condition, as they were not subject to pressure and had sufficient space for migration.

Whether originally specially nutritive or not, the wandering cells would readily become modified and change their function; their contractile power might be emphasised, and thus they might be converted into simple muscle-cells. By the secretion of mineral matter they would form skeletogenous cells. By retaining a free existence others would serve as carriers of matter, or, in other words, become corpuscles of the nutrient fluid.

Most of the internal supporting (endoskeletal) elements, with the exception of the notochord of the Chordata and the connective tissues, are, together with the blood-corpuscles and vascular system, developed from the mesoblast. Lankester has associated these series of tissues under the common designation of "skeletotrophic." This he regards as a "natural group of tissues which is divisible into—(1.) Skeletal, including fibrous, adenoid, adipose, bony, and cartilaginous tissues. (2.) Vasifactive, including capillaries and embryonic blood-vessels. (3.) Hæmolymph, including the hæma or hæmaglobinous element and lymph, the colourless element of vascular fluids."

Lankester further points out that "the mother-cells of all tissues are either 'entoplastic' or 'ectoplastic,' or both—that is to say, the metamorphosis of their protoplasm is either essentially one occurring at the surface of the protoplasmic corpuscle, or one occurring deeply within its substance, or the two processes may go on in connection with the same cell." Thus hyaline cartilage is essentially ectoplastic, while notochordal tissue results from a metamorphosis of the cells and is essentially entoplastic. "Fibrous tissue generally is ectoplastic, as the protoplasmic corpuscles remain more or less intact whilst surrounded by the fibrous and lamellar masses to which they have peripherally or laterally given origin. This is true of ordinary subcutaneous areolar tissue, of tendon, of mucous tissue (umbilical cord), and of corneal tissue. At the same time we find in various Invertebrate groups (not in the Vertebrata) an entoplastic form corresponding chemically and functionally to the ectoplastic forms just cited. This is the vesi-

cular connective tissue so abundant in the Mollusca, in the Nemertines, and other Invertebrates. The only tissue which in form represents this among the connective tissues of Vertebrates is adipose tissue." The vesicular cells of Mollusca contain glycogen; indeed, a glycogenetic function is now known to be widely distributed in various mesoblastic tissues.

"Yet further, the tissues of the connective group which are specially related to the nutrient fluids (such as blood and lymph), and which form the wall of the coelom or of blood-channels, may be entoplasmic when they give rise, by internal metamorphosis (liquid vacuolation), to capillary vessels; or ectoplasmic when they constitute spongy or lacuniferous cell aggregates, the cells separated by intercellular channels, such as we find in the 'pulp' of lymph-glands and the spleen, and in the lacunar tissue of Molluscs."

The formation of gastric pouches (archenteric diverticula) appears to have resulted from the disproportional growth of the hypoblast. In forms higher than the Coelenterates these pouches were constricted off from the central cavity and formed a true body-cavity or coelom. A nutritive fluid might collect by osmosis within the body-cavity.

The progression of the organism in a determinate direction would ensure a bilaterally symmetrical arrangement of the organs of the body, and, consequently, of the archenteric diverticula. A dorsal and ventral mesentery would result from the appression of the inner walls of the confluent lateral coeloms, while transverse mesenteries or septa would occur if the coeloms of the segments remained distinct.

The primitive nutritive corpuscles (mesamœboids) lie within the blastocoel (or, as Hubrecht proposes to term it, the archicoel), and consequently outside the archenteric diverticula. When the coelomic walls were approaching one another, many of the corpuscles would be enclosed between them; and if a small space was left between the walls of the coeloms, a tube would be formed, lying within the mesentery, containing amœboid corpuscles. The walls of the coeloms possess actual or incipient muscle-fibres, and are therefore contractile. The contractility of the walls of the mesentery would thus result in a longitudinal contractile tube containing corpuscles, in other words, a vascular system would be initiated. The development of the heart in both Vertebrates and Chaetopoda appears to support this hypothesis of its evolution.

Hubrecht claims for the blood-vascular system of the Nemertine

Worm Lineus that it arises merely by the "connective tissue" not obliterating the archicœl in these places, and that the indifferent mesoblast is modified *in situ* into the endothelium and walls of the vessels. In most other animals the smaller vessels are formed by the hollowing out of solid cell-rows and cell-groups.

It would be rash to hazard a conjecture concerning the evolution of the excretory organs until we have more precise information concerning their development in the lower Metazoa. It is not improbable that there is no genetic connection between the excretory organs (nephridia) of certain groups; thus it is difficult to see the homology in such organs as the green gland of Decapod with the excretory tubes of Amphipod Crustacea, or these again with the nephridia of Peripatus and the Malpighian tubules of Insects. The Vertebrate excretory organs appear almost certainly to have been evolved from some primitive form of nephridium, from which the nephridia of the Segmented Worms were independently differentiated.

Embryonic Digestion.—But little is known concerning digestion and assimilation in embryos. The actual processes must be assumed to be essentially similar to those occurring in adults. The following general features, which alone can be dealt with here, are worthy of notice.

As was mentioned very early in this work, an oosperm must be regarded as an amœboid Protozoon, which multiplies by fission very rapidly, but which is precluded from obtaining fresh nutriment directly. The energy requisite for this enormous activity is provided by the breaking down, through digestion, of the highly nitrogenous food-yolk which is stored up within the body of the ovum.

In many cases the stored-up nutrient material, yolk, is really derived from neighbouring ovarian cells which the ovum has swallowed. (This process, which is simply a case of feeding, must not be confounded with the formation of a plasmodium or syncytium by the fusion of previously distinct protoplasmic units.) The ovum has, in fact, gorged itself preparatory to entering upon a stage of rapid cell-division. The telolecithal and centrolecithal distribution of the yolk in the ovum and developing embryo has been already referred to. In the former case the yolk is actually stored up within the primitive hypoblast cells, that is, within those very cells whose function is to digest it. In the second case the yolk is afterwards transferred to those cells.

1. **Hypoblastic Digestion.**—The act of digestion is almost entirely performed by the hypoblast. From the nature of the case all Protozoan digestion must be intracellular, that is, must be effected within the cell itself. It is now proved that the digestion of the Cœlenterates and of some Turbellarian Worms is largely intracellular, although extracellular digestion also occurs to some extent. Even in some of the lower Vertebrates the epithelial cells of the intestine may send out pseudopodia for the purpose of ingesting fragments of partially digested food. In other words, the lower Metazoa have not yet broken away from the traditions of Protozoan digestion. In this respect early embryos of higher Invertebrates reproduce the ancestral condition; for we find in the Crustacea (fig. 22) that the hypoblast of the gastrula stage feeds upon the yolk by means of pseudopodia, and the digestion is intracellular.

Caldwell states that throughout larval life intracellular digestion occurs in the first stomach of Phoronis, but that this mode of digestion ceases when the metamorphosis takes place.

Kollmann has recently shown that in the meroblastic ova of the Lizard and Fowl (fig. 66) the primitive cells of the germinal wall, in the equivalent of the gastrula stage, engulf and digest the yolk spheres and granules like an Amœba eating its prey.

It is probable that extracellular digestion, as it occurs in the more specialised Metazoa, does not take place till "hepatic" or other secretory cells make their appearance. Most Prosobranch Molluscs, such as *Purpura* and *Fusus*, possess a large quantity of food-yolk which is stored up within the hypoblast cells (fig. 18), and the digestion of which is consequently intracellular. It is well known that during the veliger stage these Molluscs are truly cannibals and devour their weaker brethren. This new food passes into the mesenteron (archenteron), and certain of the hypoblast cells acquire a very different appearance from the remainder and constitute true digestive cells. Food in process of digestion is seen within the cavity of the mesenteron. As a matter of fact, the two modes of digestion take place simultaneously until the yolk is quite absorbed.

This view is rendered the more probable from the fact that in the Ichthyopsida the distinctive complex digestive glands are either not at all or only slightly developed. Each individual cell of the mesenteron may be regarded as individually digestive, and thus in these forms hypoblastic intracellular digestion occurs.

Temporary pseudopodia, for the seizure of food particles, are very generally emitted by the cells of the intestinal epithelium in the lower Vertebrates. Such highly differentiated glands as the peptic glands and the glands of Lieberkühn are found, from the Reptilia upwards, in an increasing degree. Their secretion acts chemically upon the whole or a portion of the food, and digests it within the cavity of the alimentary canal. The liver has been omitted in this connection, as it is not, in the true sense of the term, a digestive gland. As Wiedersheim has pointed out, there is a well-marked correlation between the folds of the mucous membrane and the development of intestinal glands. At first, as in the Cyclostomes, the folds have only a longitudinal direction, but afterwards transverse folds appear and crypts are formed in order to increase the secretory surface of the alimentary canal.

In Mammals the embryo is nourished directly by the blood of its mother, and the hypoblast of the foetus has never been functional in digestion; it consequently requires what Sollas has termed a gastric education before it can digest the food of the adult. (This argument does not apply to those Sharks and Lizards in which there is a slight connection between the yolk-sac of the embryo and the blood-vessels of the wall of the oviduct, as in these forms a large amount of food-yolk is always present.) The secretion of milk by the mother supplies a readily assimilable pabulum, and the peculiar character of the first-formed milk probably renders the education still more gradual. A somewhat similar digestive education occurs in some Birds, such as Pigeons, the Flamingo, and others.

2. Epiblastic Digestion.—The epiblast very rarely appears to have a digestive function. Metschnikoff, however, has observed intracellular ingestion by the ectoderm cells of larval Actiniae, and Kollmann states that the epiblastic cells of the blastoderm of certain Sauropsida can take up food by means of pseudopodia and digest it in the intracellular manner. It has been previously noted that villi develop from the epiblast which underlies the yolk-sac in Birds (fig. 75, B, *v*), and also from the epiblast of the allantoic folds (C, *v*), which absorb the remaining albumen of the egg. In the lower Mammals (fig. 80) similar villi occur, which must be the means of absorbing nutriment from the uterine wall.

3. Mesoblastic Digestion.—The undifferentiated wandering mesoblast cells may also be concerned in digestion, but their ingestion of foreign particles may be due in many cases to the

mechanical properties of their protoplasm rather than to an actual selection. Our knowledge concerning the behaviour of these cells in embryo Invertebrates is almost entirely due to Metschnikoff, who has proved that the mesamœboids are of great physiological importance from their first appearance, and in this respect they offer a marked contrast to the mesothelial mesoblast.

In Echinoderm larvæ, for instance, which undergo rapid metamorphoses, the disappearing organs break down into albuminoid globules, which are devoured and digested by the mesamœboids, or phagocytes, as Metschnikoff terms them. The latter also ingest small foreign particles which may be forced into the segmentation-cavity. In many cases the mesamœboids fuse to form a plasmodium or giant cell, in order to effect this more readily; in some cases the mesamœboids merely collect round the foreign body in order to isolate it.

The lymph-corpuscles (leucocytes) have been shown by Wiedersheim and by Schäfer to perform an important part in digestion in adult Vertebrates. These cells have been proved to force their way through the mucous membrane into the cavity of the intestine, and there to devour fat, and probably amyloid particles; they then return, and, crawling between the epithelium cells, pass into the lacteals. Others, again, merely ingest the food particles which have penetrated through the intestinal epithelium. In all cases, probably, the leucocytes pass into the lymphatics, where their contents are discharged by the disintegration of the cells themselves. The lymphatic fluid or chyle then passes into the general circulation, carrying with it the digested food which has been conveyed from the intestine by the leucocytes, and a large amount of proteid material derived from their dissolved protoplasm and nuclei.

It is still an open question whether digestion may not be performed in Sponges by the ectoderm as well as by the endoderm. The wandering mesoderm cells are probably concerned in the conveyance of nutriment and the removal of waste products, in addition to those functions which are more generally regarded as typical of that layer.

Closely associated with the subject of embryonic digestion is the part which the foetal membranes of Amniote Vertebrates play in nutrition. The reader is referred to the section which deals with these structures (pp. 78-96) for a summary of the evolution of the foetal membranes of the Amniota. The gradual acquisition

by the allantois of the whole of the nutrition of the embryo is especially noteworthy.

Embryonic Respiration.—The function of respiration must of necessity occur throughout the whole of embryonic and larval life. As a rule, it is more active in larvæ than in adults; at all events, the former always speedily succumb to a deficiency in the supply of oxygen.

The true respiratory process, *i.e.*, the assimilation of oxygen and the excretion of carbon dioxide, occurs in the ultimate tissues; it is only the exchange of the latter gas for the former of the external medium which occurs in what are termed respiratory organs.

As Dohrn points out, it is the vascular system which is really respiratory, and the pressure of a blood-vessel against an epithelium would cause an evagination of that tissue, be it epiblastic or hypoblastic. Of course the whole skin of the body and the alimentary tract were the primitive respiratory surfaces. The production of gill-filaments on a given area is the result of the presence of blood-vessels; it is the latter after all, and not merely epithelial prolongations, which constitute gills.

It often happens that in embryos and larval forms the delicacy of the tissues suffices for the interchange of the gases, so that special respiratory surfaces are not required. When protective envelopes are present, they are usually very permeable to gases.

The proctodæum serves as a special respiratory organ in certain larval Arthropoda; as, for instance, in the Nauplius larvæ generally, and in the aquatic larvæ of Dragon-flies.

The higher organisation of the embryos of Vertebrates necessitates a large supply of oxygen, and, consequently, special provision has to be made by the development of larval respiratory organs, especially in those forms which undergo a secluded development. These may either be (1) the phylogenetic respiratory organs, which are utilised in the ontogeny of the individual, or (2) they may bear no relation either to the ancestral or to the adult respiratory organs. A pair of examples of each of these two cases will illustrate the general principle.

1. Utilisation of Phylogenetic Respiratory Organs in Ontogeny.—The ordinary hypoblastic gills of Elasmobranchs appear early in the embryo, but the filaments on the posterior aspect of the archs are greatly elongated, so as to form a very characteristic fringe of gills, which have even been regarded as belonging to a different category from the normal filaments.

Both external and internal, *i.e.*, epiblastic (?) and hypoblastic gills occur in the newly hatched tadpoles of Frogs. Whatever may be the exact significance of the former, the latter certainly are an example of the utilisation by a larva of the ancestral mode of respiration, as the respiratory organs of the adult, in this case the skin and lungs, have no connection whatever with the former.

2. **Secondarily Acquired Larval Respiratory Organs.**—The embryonic respiration of the Amniota affords a good example of the second proposition. In none are the walls of the visceral clefts functional as gills at any time, and, as the lungs are only functional after birth, accessory respiratory organs must be provided.

In Sauropsida the area vasculosa of the yolk-sac forms the first respiratory surface, this function is next shared with the rapidly developing vascular allantois, and lastly, owing to its enormous size, the allantois becomes the sole respiratory organ. As has been mentioned above (p. 259), the allantois is probably the hypertrophied and precociously developed urinary bladder, and we may assume that the ancestral forms of the Amniota, like the Amphibia, had a large membranous vascular urocyt, which was capable of being early utilised as a respiratory organ. The topography of the allantoic blood-vessels, and the fact that the proximal portion of the allantois actually persists as the adult bladder, support this view. It is well known that egg-shells are very porous to gases.

Respiration in the embryos of the Prototherian Mammals is doubtless perfectly comparable with that in Reptilian embryos, whereas, in the Eutheria, aerial respiration is impossible owing to the embryos being included within the uterus. The foetus *in utero* has, however, no need for special organs of respiration, as it is supplied with aerated arterial blood direct from the main arterial trunks of the parent. The carbonic acid and other waste products of the embryo are carried away by the maternal venous circulation.

Evolution of Nervous System and Sense Organs.—The epiblast naturally forms the protective covering of the organism, and would readily be modified to meet special requirements. From its position it would be directly subjected to every vibration in the external medium, and would therefore be continually receiving numerous stimuli, which would call into play the sensibility of the protoplasm of the cells. It is, then, no wonder that sense-cells originated, or that these became grouped together to form sense

organs, or that a further differentiation occurred which resulted in the evolution of a highly specialised nervous system.

All these obvious facts were sufficiently noticed in the section on the "Organs derived from the Epiblast," and therefore need not be reiterated here.

Continuity of Germ-Producing Tissue.—The germ-producing tissue is to be regarded as the direct product of the similar tissue of its parent, that is to say, a portion, however minute, of germinal substance is transmitted by the parent to its offspring. The germinal substance in the latter is increased by the ordinary method of nutrition and growth, but it still has the same essential character that was transmitted to it. The offspring in its turn passes on this germinal substance. There is thus a continuity of germinal matter, which, since it is transferred in an extremely minute quantity, must have an inconceivably complex structure, as it possesses the power of transmitting hereditary characters even of the most trivial nature.

It is maintained by some that the nucleus is the essential element in the germ-cell, whether ovum or spermatozoon, and that the cell-protoplasm is merely a nutritive basis. The structure of the ovum has already been stated to be similar in many respects to that of ordinary undifferentiated tissue-cells (fig. 5*). The distinguishing feature of the nucleus over the rest of the protoplasm of the cell consists in its possession of chromatin. As the chromatin always takes a conspicuous part in segmentation, we are justified in assuming that the chromatin or nuclein is concerned in the reproductive function. Fertilisation appears to be mainly the fusion of the nuclein elements of a pair of cells which are liberated from usually two parents. The resulting compound oosperm develops by segmentation and ulterior differentiation into an organism resembling, and at the same time differing from, each of its parents both in feature and in inherited tendency.

Weismann recently proposed the view that the nucleus of every germ-cell contains "*germ-plasma*," or that substance which enables the germ-cell to build up a new individual; and "*histogenetic plasma*," or that substance which enables the germ-cell to accumulate yolk, secrete membranes, or, in short, to develop itself into its characteristic structure as a ripe ovum or spermatozoon.

It is the germ-plasma alone that is required for the development of the embryo. The histogenetic plasma, having performed its function of building up the germ-cell, is useless, and has to be got rid off; so it is extruded as the polar-cells, or as the passive element in the male germ-cells. If the germ-plasma left in the ovum has sufficient vigour (which would probably depend upon its quantity), there is nothing to

prevent its further development into a new individual—that is, nothing to hinder the occurrence of parthenogenesis. As a matter of fact, however, this is rarely the case, and it requires the sudden accession of fresh energy in the shape of a spermatozoon to enable the germ-plasma of the ovum to further develop. In this view there is no essential distinction between the nucleus of the ovum and that of the spermatozoon; the latter, like the former, is merely germ-plasm: the difference being that, as a rule, the germ-plasm of the male cell has an entirely different series of inherited characters, which it can transmit to the segmentation nucleus in the same manner as those of the female cell are transmitted.

The essential act of fertilisation, therefore, does not consist in the fusion of elements which differ in kind, but merely in the sudden accession of a store of energy which will enable the ovum to segment and build up a new individual. This brings fertilisation to resemble conjugation yet more closely; and it further explains how it is that, in those forms in which parthenogenesis is not known to occur, the ovum may segment, and proceed a short way on its development.

This theory also agrees well with certain facts concerning the asexual reproduction of animals or plants. During segmentation there is formed in the nuclei of the segmentation-cells fresh histogenetic plasma, which is more especially concerned in the differentiation of the tissues; but the germ-plasma may be generally diffused, or it may be early localised within certain segmentation-cells. Sponges, the Hydra, some Sea-Anemones, may be taken as examples of the former condition, as in these animals apparently any portion of the body containing ectoderm and endoderm will serve to produce a new individual; and in the case of the two first-named, the germ-cells themselves appear to arise indiscriminately from the mesoderm in the former, and from the ectoderm (?) in the latter. In other Coelenterata the germ-cells are of hypoblastic origin. In the second case, where the germ-plasma is localised to a special tissue, those segmentation-cells which will form the epiblast possess no germ-plasma, and, consequently, they can only build up specialised tissue. On the other hand, in most cases at all events, the germ-plasma, which at first is restricted to the nuclei of the hypoblast cells, becomes, as development takes place, still further localised until it is situated solely in that tissue which has for its especial function the reproduction of the individual. In other words, it is restricted to the generative gland. Asexual reproduction in such groups as the Polyzoa and Ascidians, and certain Worms, is rendered possible by the retention of germ-plasma within certain undifferentiated tissue (funicular tissue, stolon, budding zones, &c.), from which the whole or part of the new individual may be formed; but it is impossible to reproduce a perfect individual from any fragment containing epiblastic and hypoblastic tissue, as can be done in the case of Sponges or the Hydra. In this connection it is interesting to find, as Gruber has shown, that if an Infusorian be artificially divided, each portion will become a perfect individual. But if the dismembered portion does not possess a fragment of the original nucleus, the animal thus produced lacks the power of reproduction. It is perfect in every respect, except that it is deprived of the germ-plasma, which alone possesses the reproductive function.

Geddes has recently discussed the theory of growth, reproduction, sex, and heredity in terms of the metabolism of protoplasm. "Protoplasm is regarded as an exceedingly complex and unstable compound, undergoing continual molecular change or metabolism. On the one hand, more or less simple dead matter or food passes into life by a series of assimilative ascending changes, with each of which it becomes molecularly more complex and unstable. On the other hand, the resulting protoplasm is continually breaking down into more and more simple compounds, and finally into waste products. The ascending synthetic constructive series of changes are termed *anabolic*, and the descending disruptive series *katabolic*."

Growth.—Herbert Spencer first pointed out that in the growth of similarly shaped

bodies the mass increases as the cube of the dimensions, the surface only as the square, and applies this conception to express the occurrence of cell-division. "Thus," as Geddes expresses it, "in the growing cell the nutritive necessities of the increasing mass are ever less adequately supplied by the less rapidly increasing absorbing surface. The early excess of repair over waste secures the growth of the cell, but the necessarily disproportionate increase of surface implies less opportunity for nutrition, respiration, and excretion; and waste thus overtakes, balances, and threatens to exceed repair. Three alternatives are then possible—(1) a temporary equilibrium may be established and growth ceases, or (2) the increase of waste may bring about dissolution and death, or, still more frequently, (3) the balance of mass and surface may be restored by the division of the cell."

"Reproduction—(a) Asexual.—Continued surplus of anabolism involves growth; this growth is sooner or later checked by the preponderance of katabolism, and the most frequent alternative is the restoration of the balance by cell-division. Thus arises discontinuous growth or asexual reproduction. Budding, simple-division, and spore formation, like continuous cell-division, are simply different forms of the necessary separation which must occur at the limit of growth if the continuity of life is to be preserved. Like continuous cell-division, asexual reproduction occurs when waste or katabolic processes are in the ascendant. But what holds true in the growth of the individual cell is valid also in regard to the aggregate. There, too, a limit of growth must eventually be reached, when discontinuous growth in some form becomes inevitable. The essential difference is simply that at first in the unicellular individual the disintegration and reintegration entirely exhaust the organism and conclude its individual existence, while in higher forms the process becomes more and more localised."

(b.) **Sexual Reproduction.**—A comparative study of the methods of reproduction which occur amongst the lower plants and Protozoa will demonstrate that "the almost mechanical flowing together of exhausted cells, as illustrated in plasmodia, is connected through the known surviving cases of multiple conjugation with normal conjugation;" the dimorphism which marks the transition from conjugation to fertilisation, making the latter indispensable, appears very gradually. "The very gentleness of the gradation leads one to regard the two processes as analogous responses to the same physiological necessities. The same disturbance of the balance between anabolism and katabolism which results in the occurrence of asexual reproduction leads in more developed forms to the separation of the dimorphic and mutually dependent elements of sexual reproduction. As asexual reproduction occurs at the limit of growth, so a check to the asexual process involves the appearance of the sexual, which is thus still further associated with katabolic preponderance." The following illustration will suffice:—Under conditions of favourable temperature and abundant food the parthenogenetic reproduction of female Aphides can be indefinitely prolonged, while a lowering of the temperature and diminution of the food at once reintroduce sexual reproduction.

"Nature of Sex.—In attempting to define the distinctive characteristics of male and female, it is necessary to begin with the sexual elements themselves. The difference between male and female is there exhibited in its fundamental and most concentrated expression. It is in the sexual elements, indeed, that the continuity of organic life is secured, the vegetative organs being but appendages to the direct immortal chain of sex-cells. The large quiescent ovum is the result of a continued surplus of anabolism over katabolism, while the growing preponderance of katabolism must find its outward expression in increased activity of movement and in diminished size; and the natural result is the flagellate sperm-cell."

In multicellular organisms sexual reproduction makes its appearance when nutrition is checked. "Some of the cells are seen differentiating at the expense of others, accumulating capital from their neighbours; and if their area of exploitation be suffi-

ciently large, emphatically anabolic cells or ova result ; while if their area is reduced by the presence of numerous competitors struggling to become germ-cells, the result is the formation of smaller, more katabolic, and ultimately *male* cells. In the same species distinct organisms may, in the same way, become predominantly anabolic or katabolic, and may be distinguishable as completely female or male organisms.

The numerous facts which have now been accumulated prove that "such conditions as deficient or abnormal food, high temperature, deficient light, moisture, and the like, are obviously such as would tend to induce a preponderance of waste over repair—a *katabolic* diathesis ; and we have just seen that these conditions tend to result in the production of *males*. Similarly, such factors as abundant and rich nutrition, abundant light and moisture, must be allowed to be such as favour constructive processes and make for *anabolism* ; and we have just seen that these conditions result in the production of *females*."

Oogenesis and Spermatogenesis.—In the maturation of the ovum, the formation of polar cells seems rightly interpreted as an extrusion of the katabolic or male elements from the preponderatingly anabolic ovum ; the converse occurs in spermatogenesis.

Fertilisation.—According to this view of Geddes', "fertilisation is comparable to mutual digestion, and the reproductive process has arisen from a nutritive want. The essentially katabolic male cell, getting rid of all accessory nutritive material contained in the sperm-blastophore, brings to the ovum a supply of characteristic *katastates*, which stimulate the latter to division. The profound chemical differences surmised by some between the male and female elements are intelligible as the outcome of the predominant anabolism and katabolism in the two elements. The union of the two sets of products restores the normal balance and rhythm of cellular life."

APPENDIX.

APPENDIX A.

SYSTEM OF CLASSIFICATION ADOPTED, WITH ENUMERATION OF ALL THE
GENERA ALLUDED TO IN THE BODY OF THE BOOK.

PROTOZOA.

1. **Protista.**
2. **Rhizopoda.**
Lobosa (Protoplasta).—Amoeba.
Heliozoa.
&c.
3. **Corticata.**
Flagellata.—Monas Proterospongia.
Ciliata.—Paramæcium, Stylonychia, Vorticella.
&c.

METAZOA.

(Trichoplax—*incert sedis.*)

I.—PORIFERA.

1. **Calcarea.**
Calcispongia.
2. **Non-Calcarea.**
Myxospongia.
&c.

II.—CŒLEENTERATA.

A. INTENIOLÆ (HYDROZOA).

Hydromedusæ.

Eleutheroblastea.—Hydra.
Gymnoblæstea (Ocellata).
Calyptriblæstea (Vesiculata).—Obelia, Clytia, Eutima, Mitrocoma,
Æquorea.
Trachymedusæ.—Cunina, Æginura, Geryonia, Carmarina.
Hydrocorallina.
Siphonophora.

B. TÆNIOLÆ.

1. Scyphomedusæ.

Discomedusæ (Acraspeda).—Aurelia, Pelagia.

&c.

(ACTINOZOA).

2. Hexactinise (Zoantharia).

Malacozoa (Actinise).—Edwardsia, Peachia, Anthea, Cerianthus.

Hexacoralla (Madreporaria).

Antipatharia.

3. Octactinise (Alcyonaria).

Alcyoniidæ.

Gorgoniidæ (Isidinæ).

Coralliidæ.—Corallium.

&c.

C. CTENOPHORA.

III.—ECHINODERMATA.

1. Pelmatozoa.

Crinoidea.

2. Echinozoa.

Asteroidea.—Asterias, Leptychaster.

Ophiuroidea.—Ophiacantha.

Echinoidea.—Echinus, Toxopneustes, Strongylocentrotus,
Hemiaster.

Holothuroidea.—Psolus.

IV.—VERMES.

1. PLATYHELMINTHES.

Turbellaria.—Planaria, Leptoplana

Nemertea.—Lineus.

Trematodoa.

Cestoda.

2. ROTATORIA.

3. NEMATHELMINTHES.

Nematoda.—Ascaris, Cucullanus.

Onstognatha.—Sagitta.

4. ANNELIDA.

Discophora.—Hirudo.

Chætopoda.

Achæta.

Polychæta.—Serpula.

Oligochæta.—Criodrilus, Rhynchelmis (Euaxes),
Lumbricus.

5. PODAXONIA.

Gephyrea.

Polyzoa.—Phoronis.

Brachiopoda.—Argiope.

V.—MOLLUSCA.

I. ODONTOPHORA.

1. Gasteropoda.

1. *Isopleura* (*Amphineura*).*Neomenia*.—*Neomenia*, *Proneomenia*.*Chætodermæ*.*Polyplacophora*.—*Chiton*.2. *Anisopleura*.A. *Streptoneura*.—1. *Zygobranchia*.—*Haliotis*, *Fissurella*, *Patella*. 2. *Azygobranchia*.—(a) *Prosobranchia*.—*Ianthina*, *Paludina*, *Ampullaria*, *Nassa*, *Purpura*, *Buccinum*, *Fusus*, *Murex*. (b) *Heteropoda*.B. *Euthyneura*.—1. *Opisthobranchia*.—*Aplysia*, *Elysia*, *Fiona*. 2. *Pulmonata*.—*Helix*, *Limax*, *Onchidium*, *Planorbis*, *Lymnæus*.II. *Scaphopoda*.—*Dentalium*.III. *Acropoda*.1. *Pteropoda*.2. *Cephalopoda*.A. *Tetrabranchiata*.—*Nautilus*.B. *Dibranchiata*.—1. *Decapoda*.—*Sepia*, *Loligo*.2. *Octopoda*.—*Octopus*.

II. ACEPHALA.

Lamellibranchiata.*Isomya*, *Anodonta*.*Heteromya*, *Dreissena*.*Monomya*, *Pecten*, *Spondylus*.

VI.—ARTHROPODA.

I. CRUSTACEA.

A. ENTOMOSTRACA.

Phyllopoda.*Ostracoda*.*Copepoda*.—*Cyclops*.*Cirripedia*.

B. LEPTOSTRACA.

Nebaliidæ.

C. MALACOSTRACA.

Arthrostraca (*Hedriophthalmata*).*Amphipoda*.*Isopoda*.—*Asellus*.

Thoracostraca.*Cumacea.**Stomatopoda.**Schizopoda.*

Decapoda.—(Carididae), Crangon, Hippolyte, Palæmon;
Callinassa; Astacus; Palinurus; Birgus;
(Brachyura), Cancer.

II. ARACHNIDA.**A. Hæmatobranchia.***Xiphosura.*—Limulus.**B. Xerobranchia.***Scorpionida.*—Scorpio.*Pedipalpida.**Araneida.***C. Lipobranchia.***Acarinida*, &c.**III. PROTRACHEATA.***Peripatida.*—Peripatus.**IV. MYRIAPODA.****V. INSECTA (HEXAPODA).***Thysanura.**Orthoptera.*—Blatta.*Pseudoneuroptera.*—(Libellulidae.)*Hemiptera (Rhynchota).*—Aphis.*Neuroptera.**Coleoptera.*—Dytiscus.*Diptera.*—Musca.*Lepidoptera.**Hymenoptera.***VII. CHORDATA.****I. HEMICHORDATA.***Enteropneusta.*—Balanoglossus.**II. UROCHORDATA (TUNICATA).**1. *Perennichordata.*—Appendicularia.2. *Caducichordata.***III. CEPHALOCHORDATA (HYPOCHTHYES).***Pharyngobranchii.*—Amphioxus.**IV. VERTEBRATA (CRANIATA).****I. CYCLOSTOMI (MYZICHTHYES).***Marsipobranchii.*(a) *Hyperotreta.*—Myxine, Bdellostoma.(b) *Hyperoartia.*—Petromyzon.

II. GNATHOSTOMATA.

A. ICHTHYOPSIDA.

1. CHONDRICHTHYES.

Holocephali.—Chimæra.

Elasmobranchii (Selachii).—(Notidanidæ), Notidanus, (Hexanchus and Heptanchus); Cestracion, Acanthias, Scyllium; Raja, Torpedo, Pristiurus.

2. OSTEICHTHYES.

Ganoidei.

Selachoides.—Acipenser, Polyodon.

Teleostei.—Polypterus, Lepidosteus, Amia.

Teleostei.

Lophobranchii.

Plectognathi.—(Gymnodontes.)

Physostomi.—(Murænidæ), Amphipnous, (Leptocephalus); Mormyrus; (Salmonidæ), Mallotus, Osmerus, Salmo, Trutta; (Cyprinidæ), Cyprinus; Cobitis; Anableps; (Siluridæ), Saccobanchus.

Anacanthini.—(Pleuronectidæ.)

Acanthopteri.—Trigla, Anabas, Lophius.

3. HERPETICHTHYES.

Dipnoi.—Protopterus.

4. AMPHIBIA.

Urodela.—(Perennibranchiata), Siren; (Axolotl); (Caducibranchiata), Amblystoma, Triton, Salamandra, Salamandrina, Gyrinophilus, Ranodon.

Gymnophiona.—(Cœciliidæ) Cœcilia.

Anura (Batrachia).—Pipa, Dactylethra; Rana, Alytes, Bombinator, Bufo, Rhinoderma; Notodelphis, Nototrema, Hylodes.

(AMNIOTA.)

B. SAUROPSIDA.

1. REPTILIA.

Chelonia.—Trionyx, Aspidonectes, Testudo.

Lacertilia.—Hatteria, Chamæleon, Gecko, Calotes, Leiodera, Scincus, Anguis, Cyclodus, Seps, Lacerta, Trachydosaurus, Varanus.

Ophidia.

Crocodylia.

2. AVES.

Ratitæ.

Struthiones, &c.

Carinatae.*Chenomorphae*.—Anser, Anas, Phœnicopterus.*Alectoromorphae*.—Gallus.*Columbae*.—Columba.*Coracomorphae*.—Pyrrhula, Luscinia, Sylvia.*Psittacomorphae*.—Psittacus.

&c.

C. MAMMALIA.**1. PROTOTHERIA (ORNITHODELPHIA).****Monotremata.**—Ornithorhynchus, Echidna.**2. METATHERIA (DIDELPHIA).****Marsupialia.***Glyrina* (*Rhizophaga*).*Macropoda* (*Poephaga*), Macropus.*Scandentia* (*Carpophaga*).—Phascolarctos, Phalangister.*Rapacia*.—Perameles, Didelphys.**3. EUTHERIA (MONODELPHIA).****Edentata.***Pilosa*.—Myrmecophaga, Cyclothurus.*Loricata*.—Dasypus.*Squamata*.—Manis.*Tubulidentata*.**Sirenia.****Cetacea.**—Phocæna.**Ungulata.***Artiodactyla*, *Suina*.—Sus, *Tragulina*, Tragulus; *Tylodactyla*; *Pecora* (Cervidæ), Moschus; Camelopardalis; Antelope, Tetraceros, Ovis, (Bovidæ) Bos.*Perissodactyla*.—Equus, Rhinoceros.*Hyracoidea*.—Hyrax.*Proboscidea*.—Elephas.**Rodentia.***Duplicidentata*.—Lepus.*Simplicidentata*.—Arvicola, Mus, Cavia.**Chiroptera.****Insectivora.**—Talpa.**Carnivora.***Pinnipedia*.—(Phocidæ).*Fissipedia*.—Mustelus, Canis, Felis.**Primates.***Lemuroidea*.*Anthropoidea*.—Homo.

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